

Stone curlews *Burhinus oedicnemus* and human disturbance: effects on behaviour, distribution and breeding success

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Author's declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text.

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Summary

Previous studies have found that disturbance of birds by human activities can result in changes in behaviour, resource use and productivity. Changes in rights of public access through the Countryside and Rights of Way Act 2000 mean that much of the preferred open habitat of the stone curlew *Burhinus oedicnemus* in southern England is now designated as ‘open access’ for recreation. Consequently, there is concern that increased human activities near stone curlew breeding sites could impact the population.

Systematic recording of behaviour showed that stone curlews respond to potential disturbance agents (PDAs) at large distances compared to many other birds. Responses varied with PDA type, time in the season, distance to PDA, and other factors. Logistic models were created that predict the probability of an active response (running or flying in response to a PDA event) being observed, in relation to attributes of the PDA. The models were then used to estimate the probability of response to any given specified PDA event. From this, the rate of responses per hour to an observed set of PDA events could be calculated.

The main effect of disturbance on stone curlews in this study area was prevention of birds settling to breed in habitat that is suitable in other respects. Models predict that where there is no disturbance, the probability of site occupancy is 60%. However, with one expected active response per hour this is reduced to a 15% probability of site occupancy.

Colour ringed pairs were observed moving from apparently suitable nesting sites where disturbance event rate exceeded 1.5 disturbance events per hour or 0.4 expected active responses per hour, and they selected a less disturbed site to breed. The average distance moved was 1.5km, although an extreme distance of 9km was observed where there were few other alternative sites. First egg date of pairs that moved was later by nine days and two pairs failed to breed that season.

There was a suggestion that chicks grow slower on sites with disturbance but this had no impact on chick survival in the longer term. There were no other clear effects of disturbance on breeding success for the whole study area over two years of data collection. However, as stone curlews were already selecting the least disturbed sites to breed, variation in disturbance on breeding sites was low and any effects may not have been apparent.

In order to guide conservation and habitat management whilst allowing recreational access, a management tool was developed from the behaviour and site occupancy models. The tool uses the models to calculate the reduction in probability of site occupancy under different disturbance intensities and offers a method to assess the effects of scenarios for future changes in disturbance type, routes and frequency. It is hoped that the tool will be valuable in making informed decisions about access and habitat creation to maximise stone curlew conservation.

Contents

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“It is singularly shy and avoids the presence of human beings, whether sportsmen or labourers. Yet it is not destitute of courage, as it has been seen to defend its nest with vigour against the approach of sheep or even of dogs.

Before taking their departure southwards in autumn, they assemble in small parties...when they are somewhat more easy to approach...and here, by the aid of a light-cart, fowlers in quest of them have little difficulty in shooting large numbers, the birds being less afraid of the approach of a horse than a human being. But when obtained they are of little value, as their flesh is barely eatable”.

The Rev. C. A. Johns, 1909

British Birds in Their Haunts

1 General introduction and aims of thesis

1.1 Human disturbance of birds

Human access to the countryside is of great importance to nature conservation because it increases public appreciation of nature, which may potentially lead to improved protection. In an increasingly fragmented and human dominated landscape, however, the relationship between conservation and human activities needs careful assessment. Human disturbance has been considered to be a major factor in the declines of many species according to the two key texts documenting bird populations in the United Kingdom (Batten *et al.*, 1990) and Europe (Tucker and Heath, 1994). Human disturbance is reported as being a potential factor in population declines of a number of species, e.g. red-throated diver *Gavia stellata*, black kite *Milvus migrans*, Kentish plover *Charadrius alexandrinus*, nightjar *Caprimulgus europaeus* and chough *Pyrrhocorax pyrrhocorax*. Specifically, 42% of red data book birds in the UK are classified as at risk from disturbance (Batten *et al.*, 1990) and 27% of the Species of European Conservation Concern (Tucker and Heath 1994). However, despite the vast amount of disturbance literature published in recent years, there is very little evidence to support these claims.

Studies of human disturbance on animals vary vastly in their subjects, objectives, methods and conclusions and very few address long term effects due to difficulties in measuring responses and fluctuating levels of disturbance over long periods of time. The coverage of major habitat types and species is patchy and uneven and many papers on disturbance contain speculative conclusions and can be misleading in the amount of emphasis that is placed on recreational disturbance (Sidaway, 1990). In particular, there is a lack of clear evidence for human disturbance being responsible for limiting populations or causing population declines. The reason for this is that most disturbance studies are not easily interpreted for the species concerned even at a local level, and so cannot easily be extrapolated to the population level or translated to other species and habitats.

Disturbance can be defined as a deviation in an animal's behaviour from patterns occurring without human influence (Frid and Dill, 2002). Gill and Sutherland (2000) consider two components to disturbance. Firstly, whether the disturbance causes animals to avoid areas that they would otherwise use in the absence of disturbance; and secondly, whether this affects mortality, reproductive success and ultimately population size.

By far the commonest method of measuring the effects of disturbance on animals has been by looking at the immediate behavioural response to disturbance (e.g. Burger and Gochfield, 1991, Thomas *et al.*, 2003). These types of studies are quick and easy to carry out as there is usually an obvious change in behaviour that can be associated with the disturbance. Many consider response distances (e.g. Arroyo and Razin, 2006, Gonzalez *et al.*, 2006, Yalden and Yalden, 1990, Rodgers and Schwikert, 2002, Stillman and Goss-Custard, 2002), time spent being vigilant to disturbance (Fernandez-Juricic and Telleria, 2000, Fitzpatrick and Bouchez, 1998), time spent away from nests or chicks (Yalden and Yalden, 1990, Verhulst *et al.*, 2001, Yasue and Dearden, 2006, Lord *et al.*, 2001), reduced feeding time (Burger and Gochfield, 1991, Thomas *et al.*, 2003) or even intensity of vocalisation (de Villiers *et al.*, 2005). Other studies consider the physiological responses which may occur through changes in behaviour as a result of disturbance such as increased heart rate (Giese, 1998, Weimerskirch *et al.*, 2002, de Villiers *et al.*, 2006), or the secretion of stress hormones (Fowler, 1999).

Human disturbance can be considered to have similar effects as predation risk for animals (Frid and Dill, 2002). When disturbed, the response of an animal is likely to follow the same economic principles used by prey when encountering predators, and the response will be a trade-off between remaining in the area and the cost of leaving. Thus, there is evidence that birds shift their tolerance to disturbance depending on the perceived risk (Walther, 1969, Ydenburg and Dill, 1986, Beale and Monaghan, 2004), their physical condition (Beale and Monaghan, 2004, Gill *et al.*, 2001), alterative resource availability (Owens, 1977), and competition (Gill *et al.*, 1996).

However, studies that do not go beyond the immediate behaviour effects of disturbance have been criticised for only considering the short term response which may not translate into any additional consequences or long term effects on the population (Gill *et al.*, 2001). For example, disturbance may cause birds to fly away from the source of disturbance but they may be able to compensate for, say, reduced foraging time, by feeding when disturbance levels are lower (e.g. Burger and Gochfield, 1991), or they may return soon after the disturbance event without any obvious costs. Although the concern over behavioural studies is valid and caution should be taken concerning the interpretation of behavioural studies (Gill *et al.*, 2001), they remain the first measure of a species' sensitivity to disturbance by human activities and can be useful in certain management situations such as determining set-back distances and buffer zones from which disturbance is limited (Blumstein *et al.*, 2005).

A second approach to measuring the effects of disturbance is by comparing animal distributions between sites with differing levels of disturbance. For example, Madsen's (1998) 12-year study of hunting in two Danish wetlands showed that refuges from hunting increased species diversity and density, and van der Zande (1984) showed that the density of birds in Dutch sand dunes was negatively correlated with visitor density. The interpretation of studies of this kind are difficult, however, because species distribution may be influenced by a variety of unmeasured factors such as prey density, territory locations, competitor or predator densities, or availability of nest sites (Gill *et al.*, 2001); furthermore, disturbance may just be causing individuals to distribute themselves further from the disturbance source rather than more generally across the habitat, and again no additional consequences or long term costs may occur. Therefore an important aspect of distribution studies is to ascertain whether human activity actually reduces the number of birds a site can support. For example, Gill (1996) measured the amount of food available (of immobile prey) at the beginning and end of a season and ascertained that pink-footed geese *Anser brachyrhynchus* used fields more frequently for feeding if they were situated further from a source of disturbance. Using the relationship between prey availability and disturbance they were able to estimate the additional number of geese that could be supported by the food resource in the absence of the disturbance.

In areas where the most disturbed habitat is not avoided altogether for breeding, many studies have quantified the effect of human disturbance by comparing breeding success between areas of high and low disturbance (see review by Hockin *et al.*, 1992). A number of studies have been able to show that human disturbance results in a reduction in measures of breeding productivity such as nest success and chick survival. Mechanisms for reduced breeding success through disturbance include: direct losses of nests and chicks by trampling (Strauss, 1990, Yalden and Yalden, 1990, Keedwell, 2001), a shift in behaviour which results in reduced foraging, reduced parental brooding, and increased exposure to predators and weather conditions (Flemming *et al.*, 1988, Straus, 1990, Yalden and Yalden 1990), brood movement away from disturbed areas which results in reduced quality of foraging habitat (Yalden and Yalden, 1990) or competition with other groups of birds (Yalden and Yalden 1990), attraction of predators (Jokimaki and Huhta, 2000, Sieving, 1992, De Santo and Willson, 2001), and increased predation when eggs or chicks are left for long periods of time (Giese, 1996).

Few disturbance studies, however, have been able to predict the consequences of human disturbance beyond the local population. Those that have been successful in doing so have

needed to incorporate a measure of density dependence (West *et al.*, 2002, Liley, 1999, Mallord, 2005). Density dependence plays a vital role in regulating wildlife populations through, for example, competition for a limited resource such as feeding sites or breeding space (Lack, 1954). An understanding of density dependence operating within a population is vital for the ability to predict the long term population consequences of a change in conditions, such as habitat loss or increased human disturbance (Sutherland and Norris, 2002).

West *et al.* (2002) used an individual-based model, incorporating data on resource depletion and interference competition, for oystercatchers *Haematopus ostralegus* feeding on mussel beds to predict the population consequences of the energy and lost feeding time incurred through disturbance in the non-breeding season. The model predicted that the time and energy costs arising from disturbance could be more damaging than permanent habitat loss. Similar studies by Goss-Custard *et al.* (1995) and Stillman *et al.* (2001) using the same modelling approach can predict the density-dependent mortality and survival arising from habitat loss and disturbance through shell fishing.

Only two studies have incorporated density-dependent population regulation into the effects of disturbance on breeding birds. Liley (1999) found that ringed plovers *Charadrius hiaticula* tended to avoid settling on the most heavily disturbed parts of a beach, resulting in displacement of birds and elevated densities in quieter areas. This resulted in density-dependent breeding success and by calculating per capita breeding success relative to density-dependent mortality; Liley was able to predict how the population size would change in response to changing levels of human disturbance. A complete absence of disturbance was predicted to allow the population to increase by 85%. However, this approach assumes that the most disturbed sites will never be occupied by the birds. If this is not the case and any breeding success in the most disturbed sites is greater than zero, the model will overpredict the effects of disturbance on population size.

In a second study, incorporating density dependence in the breeding season, Mallord (2005) showed that the density of woodlarks *Lullula arborea* on more disturbed Dorset heathland sites was lower as a result of disturbance causing suitable habitat to be avoided. However, woodlarks on more disturbed heaths had greater density-dependent reproductive success, including recruitment into the local breeding population.

1.2 Management of disturbance

Where human disturbance has a detrimental effect on birds, the amount of visitation may need to be managed temporally or spatially. For example, exclusions may be made at certain times of the breeding season (Richardson and Miller, 1997, Ronconi and St. Clair, 2002) or day (Ronconi and St. Clair, 2002). Often flight distances are used to set exclusion areas or buffer zones within which there is no human activity (Rodgers and Smith, 1995, Rodgers and Schwikert, 2002). Alternatively, redistribution of routes of disturbance away from certain areas may be possible (Fernandez-Juricic, 2000, Fernandez-Juricic *et al.*, 2003), which may be more desirable, because the overall number of people allowed to use the site need not be reduced. There is also evidence that the presence of a fence between animals and disturbance can reduce any behavioural effects of disturbance (Ikuta and Blumstein, 2003), and also makes direct destruction of nests less likely (Burger *et al.*, 1995).

Enforcement of management can be costly and time consuming and it may also lead to conflicts between recreational users and nature conservation. Furthermore, usually, the most appropriate management is site and species specific. It is therefore important that management can be justified through high quality research, and delivered to benefit both nature conservation and recreational users of the countryside (Sidaway, 1990).

1.3 Changes in countryside access

The issue of human disturbance and wildlife conservation has become increasingly relevant in England and Wales with changes in access rights. After decades of campaigning by the Rambler's Association for increased access to the countryside, a new law was finally passed in 2000 which gives new rights of access off public rights of way. The Countryside and Rights of Way Act 2000 (CRoW) aimed to extend the public's ability to enjoy the countryside through creating a new statutory right of access and modernisation of the rights of way system (<http://www.opsi.gov.uk/Acts/>). Despite being given the alternative name 'Right to Roam' by many, CRoW is restricted in its extent and only applies to mapped areas of uncultivated, open countryside namely mountain, moor, heath, down and registered common land in England and Wales. Furthermore, the Act gives access for recreation on foot only, excluding vehicles, horse riders and cyclists.

Within the Act there is provision for safeguards to take account of the needs of landowners and managers and of other interests, including wildlife (<http://www.defra.gov.uk/wildlife->

countryside/ci/index.htm). As a result, access to land covered by the new rights can be restricted under some circumstances. Landowners can restrict or exclude the public from their land for up to 28 days each year for any reason and also during times when it is deemed necessary for land management, fire prevention, or public safety. There are also requirements within the Act to control dogs on CRoW land. There is a general requirement for dogs to be kept on a short fixed lead of no more than two metres in length between 1 March and 31 July in an attempt to protect ground nesting birds, and at any time in the vicinity of livestock. There is also provision for further temporary or permanent closures or restrictions to take account of the needs of conservation, land management, defence and national security, and safety.

Any closures and restrictions for wildlife conservation, however, should be justified and supported by clear evidence of the adverse effects of disturbance. During the public consultation period for the Act it became clear that potentially vulnerable species should be identified and a strategy drawn up for disturbance research in the key habitats affected (Liley, 1999). As a result, several species were identified as being potentially vulnerable under the CRoW Act. These were mostly scarce, habitat restricted, ground nesting species and included the stone curlew *Burhinus oedicnemus*.

1.4 Stone curlew ecology, distribution and population trends in England

1.4.1 Stone curlew ecology and breeding behaviour

The stone curlew *Burhinus oedicnemus* (L.) (Charadriiformes: Burhinidae) is a migrant wader to the UK. It is mostly crepuscular and nocturnal and nests and forages in sparsely vegetated areas (Green and Griffiths, 1994) where it relies on its cryptic markings to avoid detection. Stone curlews are ground nesting, selecting areas of short and sparse vegetation in open areas to create a nest scrape of around 20 cm in diameter, which is often decorated with an elaborate display of small stones, shells, rabbit droppings and small pieces of vegetation (Cramp and Simmons, 1983). Two egg nests are the norm although single eggs regular occur and three egg nests have been observed a small number of times (including within the duration of this study). Incubation lasts on average 27 days, shared by both sexes (Cramp and Simmons, 1983). Young are precocial and nidifugous and are cared for by both parents until fledging at 36-42 days (Cramp and Simmons, 1983). Replacement nests occur after failure at both the egg and chick stage and stone curlews can also be double brooded. Data from recoveries of ringed stone curlews show that 61% of juveniles survive in their first year and subsequent annual survival is 83% (Green, Hodson and Holness, 1997). With these survival rates, 0.61 young need to be fledged per pair per year for the

population to be maintained (Green, Hodson and Holness, 1997). After breeding ends in late August and September, large roosts form at traditional sites before migration back to wintering grounds in late September. At this time adults undergo a full body moult and juveniles continue moulting into adult plumage.

The stone curlew diet consists mostly of soil invertebrates and surface dwelling arthropods (Green and Griffiths, 1994, Green, Tyler and Bowden, 2000, Amat, 1986, Green and Tyler, 1989), although birds' eggs, small mammals, and apparently the occasional toad are reportedly also taken. Chicks are fed a large amount of earthworms when young, particularly in wet springs (Green, Tyler and Bowden, 2000), which probably contributes to increased growth.

Early investigations of breeding behaviour by the likes of Walpole-Bond (1938) and Ogilvie (1920) have been supplemented in recent years by intensive studies by R.E. Green and others in England. As a result we now have very detailed information on habitat requirements (Green *et al.*, 2000), nocturnal ranging behaviour (Breen *et al.*, 2000), diet (Green and Griffiths, 1994), breeding parameters (Bealey *et al.*, 1999) and survival and movements (Green, Hodson and Holness, 1997) of stone curlews. Furthermore, Martin and Katzir (1994) provide detailed information about visual fields and Day (2003) reports on the effects of major roads on stone curlew population in Breckland.

1.4.2 Stone curlew distribution

The global range of the stone curlew extends from North Africa and Iberia, east through southern Europe to Central Asia, India and south-east Asia (Cramp and Simmons, 1983), with between a quarter and a half of the population (estimated at between 32,690 - 45,704 breeding pairs) occurring in Europe. Within the range, northern populations are migratory, whilst the southern, tropical and sub-tropical populations appear sedentary. Recoveries of stone curlews ringed as chicks in southern and eastern England show that English birds migrate through western France and winter in Spain, Portugal, Morocco and West Africa (Green *et al.*, 1997).

Stone curlews are polytypic and six sub-species have been recognised. The nominate race *Burhinus oedicnemus oedicnemus* inhabits England at the far north-western edge of its global range, and is confined to two populations in central southern England and East Anglia. Cross-over of individuals between the two English populations does occasionally occur (Green *et al.*, 1997), but the two areas may generally be considered separate. The larger of the two populations

is centred on the Breckland of Norfolk and Suffolk (known as the Breckland sub-population), where in 2005 the breeding population was approximately 200 pairs. The other population of stone curlews in England is in Wiltshire, Hampshire and Berkshire, centred on Salisbury Plain and Porton Down, and is collectively referred to as the Wessex sub-population. The breeding population in Wessex in 2005 was approximately 100 pairs.

Stone curlews breed almost exclusively on habitats with free-draining stony soils, good visibility of the surrounding area and bare ground or a short sward height maintained by rabbit or livestock grazing. The main habitat for breeding in Breckland is sandy heath and spring sown cereals, although very young or recently felled forestry is occasionally used. In Wessex, the traditionally habitat is lowland calcareous (chalk) grassland which has developed on shallow lime-rich soils overlying limestone rocks. However, loss of traditional habitats in the Wessex area has resulted in most pairs of stone curlews nesting on artificial, specially created stone curlew nesting plots.

1.4.3 Long term population decline of stone curlews

In the UK, the stone curlew was formerly more widespread beyond its current range, with birds breeding on all light soils north to the Yorkshire Wolds. However, the species suffered a long-term decline in numbers and range mostly as a result of habitat loss and deterioration (<http://www.ukbap.org.uk/ukplans>). Population estimates pre-1930 are not known, but by the late 1930s the population was likely to be around 1000-2000 pairs (Batten *et al.*, 1990). Subsequent estimates were 200-400 pairs in the 1960s (Parslow, 1973), 300-500 pairs in the early 1970s (Sharrock, 1976) and 150-160 pairs in the early 1990s (Gibbons *et al* 1993). Range wide population declines have also occurred, with stone curlews now extinct from several European countries where they formerly bred, for example the Netherlands (Cramp and Simmons, 1983). As a result of long term declines and contraction of range, stone curlews benefit from a large amount of protection (<http://www.ukbap.org.uk/ukplans>). During the breeding season they are protected under Schedule 1 of the Wildlife and Countryside Act 1981. They are also a UK Species of Conservation Importance and a Species of European Conservation Concern where they are classed as vulnerable. Furthermore, wintering birds in Europe are protected under Annex 1 of the EC Birds Directive 1979.

1.4.4 Factors associated with the decline in England

The major factor in the decline of the Wessex stone curlew population was the reduction in the area and quality of lowland calcareous grassland due to agricultural intensification and drastically

altered farming patterns since the 1940s (<http://www.ukbap.org.uk/ukplans>). In particular, intensive arable cultivation has increased and alongside, a dependence on fertilisers and herbicides to boost yields. As a result, much of the traditionally managed chalk downland has been converted to arable crops. At the same time in the UK, livestock farming underwent changes. Arable farming is no longer so intimately linked to stock rearing, and cattle and sheep farming in themselves have become much more intensive. Stocking rates are higher and there is less flexibility in grassland management. Sheep, and to a lesser extent, cattle rearing were important aspects in the formation and maintenance of the chalk grassland landscape. Over the summer, animals were grazed on downland but folded onto arable land at night to manure it. This removed nutrients from the grassland, exacerbating its natural low fertility and promoting herb-richness (<http://www.ukbap.org.uk/ukplans>). Grazing by livestock at low densities also contributed to the maintenance of the short sward suited to stone curlews. However, it was mostly rabbit grazing and burrowing activity that kept patches of grassland very short and with bare areas suitable for breeding by stone curlews, but the rabbit population crashed after the myxomatosis epidemic in the 1950s.

In the absence of suitable semi-natural chalk grassland for nesting, stone curlews exploited (and still do today) arable crops, although at much lower densities than on semi-natural grassland (Green and Griffiths, 1994). Here, nests were vulnerable to several factors which remain problems today. Firstly the switch from spring to winter sown cereals has meant that many crops are unsuitable for nesting by the time stone curlews return from wintering grounds in March. Today, even spring cereals are being sown earlier and often quickly become unsuitable for stone curlews in terms of crop height and density. This has meant that the time period available with suitable habitat is so reduced that there is often no time to complete a brood. Furthermore, even if first broods are possible, rarely can the crop provide suitable habitat for second broods or relays after failures (Green and Griffiths, 1994). Secondly, many crops are now sprayed or rolled at stages in the growth, which leads to nests or chicks being lost to machinery.

Two large areas of chalk grassland that escaped the pressures of agricultural intensification are Salisbury Plain Training Area (SPTA) and Porton Down. Owned by the Ministry of Defence (MoD), these huge tracts of downland have been largely isolated from agricultural intensification, as their management has been dictated by military use. At 19689 ha, SPTA is now the largest single area of chalk grassland in Western Europe and as a result, its significance to nature conservation is outstanding. In recognition of this, SPTA has been designated a Special Area of

Conservation (SAC), Special Protection Area (SPA), and Site of Special Scientific Interest (SSSI). Porton Down, whilst smaller (1227 ha) is still one of the largest remnants in the UK and is also of international importance.

Porton Down is currently the only semi-natural chalk grassland site that stone curlews regularly breed on, and supports around 25 pairs annually. Where stone curlews nest on grassland on SPTA they are exploiting areas where vehicular disturbance has created a short sward. Grazing and cutting of the grassland and the rabbit grazing pressure on SPTA is no longer intensive enough to provide other suitable semi-natural nesting habitat.

1.5 RSPB Stone Curlew Recovery Project

In response to the stone curlew population decline, a RSPB/English Nature recovery project was established in both Breckland and Wessex, beginning in the mid-1980s. The recovery project aimed to protect crop-nesting stone curlews from the adverse effects of agricultural operations on breeding success by finding and protecting nests and chicks. It also sought to expand the area of habitat not subject to agricultural operations by providing more areas with short, sparse vegetation on thin, stony soils. This was achieved in part in Wessex through the establishment of stone curlew nesting plots, 1-2 ha areas of cultivated land within semi-natural grassland or arable crops which provide the bare, stony habitat favoured by stone curlews (Green and Griffiths 1994, Green and Taylor 1995, Green *et al.* 2000).

Stone curlew plots are created under state-funded schemes such as derogated set-aside, agri-environment schemes such as Habitat Scheme, Countryside Stewardship or the new Environmental Stewardship Entry- and Higher-level schemes (www.defra.gov.uk) and initiatives by the statutory nature conservation agency, English Nature, which funds plots through the Wildlife Enhancement Scheme. In addition, nesting plots have been created by the MoD on military training areas, and by conservation organisations such as the RSPB and Norfolk Wildlife Trust. The location of some types of plot varies from year to year, but the majority are permanent and are prepared each season prior to the birds' return from wintering grounds, by shallow cultivation to provide a bare area.

As a result of the data collected by the RPSB Stone Curlew Recovery Project, since 1987 we have details of all known nesting attempts and all known chicks have been colour ringed, giving a population of breeding birds where around 80% of birds are individually marked.

1.6 Aims of the thesis

We know in detail the habitat requirements for stone curlews and as a result the creation of suitable artificial nesting plots has assisted in the population recovery. The creation of nesting plots is relatively simple and has been very successful and is therefore a highly effective solution to the problem of habitat loss for stone curlews. However, the creation of plots can be expensive and their potential use must be maximised. Beyond providing a suitable substrate for nesting, ensuring feeding habitat close by, and avoiding main roads (Day, 2003) we know little else about where to place plots in the landscape to maximise success. However, conservation measures are likely to be more successful if based upon detailed information on the species' natural history and scientific studies of causes of its rarity (Caughley, 1994). Therefore, continuing research to improve stone curlew conservation is vital for the long term survival of the species as a breeding bird in England.

There is anecdotal evidence that stone curlews move away from human walkers at long distances and avoid disturbed areas when nesting and roosting. With the CRoW Act and potential changes in military training, several areas of stone curlew habitat may be put under increased pressure from human disturbance and the potential effects on stone curlews are not clear. Increased disturbance may lead to alterations in settlement and distribution, with seemingly suitable stone curlew habitat avoided in areas where disturbance is high. Disturbance could also affect breeding productivity and so have an impact at the population level.

Therefore, the overall aim of the thesis is to establish if and how disturbance is affecting the present stone curlew population in Wessex in terms of settlement, distribution, behaviour and breeding success; and how access and stone curlew conservation can be managed to benefit both.

1.7 Structure of thesis

In **Chapter 2** I show characteristics of the breeding area with respect to disturbance, model disturbance in relation to potential disturbance correlates in an attempt to produce a model to predict disturbance on stone curlew sites, and assess the ability of land managers to estimate levels of disturbance. I then concentrate particularly on three areas that I considered may be affected by human disturbance: stone curlew behaviour, site use and breeding success. Stone curlew behaviour in response to human disturbance is considered in **Chapters 3, 4 and 5**. Firstly, **Chapter 3** shows response distances and responses to disturbance events and I discuss how

results can be used in the management of access. Secondly, **Chapter 4** introduces a new method for measuring the effect of disturbance on behaviour based on the specific route of the disturbing event in relation to the stone curlew and results are discussed in the context of a predator risk framework. Thirdly, models in **Chapter 5** follow the methods described in Chapter 4 to provide an improved disturbance event rate based on behavioural responses which is used in subsequent chapters. **Chapter 6** relates the behavioural response of stone curlews to disturbance with the use of nesting sites and investigates how changes in the disturbance regime could affect resource usage. **Chapter 8** continues this theme by looking closely at movements of stone curlews during the sensitive settlement period pre-breeding and the subsequent costs of disturbance preventing breeding on first choice plots. In **Chapter 7** I consider the impacts of disturbance on breeding parameters where stone curlews settle to breed. Finally, management implications and recommendations and the development of a tool to help guide stone curlew conservation under the CRoW Act and changes in military training, are discussed in the General Discussion in **Chapter 9**.

The data collection methods are similar throughout the thesis and so to avoid duplication I have described each method once in the earliest chapter appropriate and then referred back to the relevant sections in subsequent chapters. Additionally, to assist with cross referencing between chapters, I have placed figures at the end of chapters.

Statistical tests were performed using S-Plus and R (Crawley 2002).

2 Potential causes of disturbance to stone curlews and factors affecting their frequency of occurrence

2.1 Summary

Disturbance events near stone curlew plots were measured in 2004 and 2005. Compared to many studies, disturbance event rate was low because of the nature of sites and placement of plots in the landscape. General disturbance and recreational disturbance including vehicles could be modelled as a function of distance to the nearest vehicle accessible road. However, the frequency of recreational disturbance excluding vehicles, and walker and dog walker disturbance could not be modelled as a function of any potential disturbance correlates such as distance to track, nearest village or access point. On Salisbury Plain Training Area, military disturbance was higher near to tracks, access points and a major training site.

In general, disturbance levels in the study area were overestimated by land managers responsible for placement of new stone curlew plots. This could have important consequences for management of access and siting of new plots. The use of the models relating disturbance levels to potential disturbance correlates could improve knowledge of disturbance levels but probably only when military or vehicle disturbance is being considered.

2.2 Introduction

Human disturbance can be defined as activities which cause a change in the behaviour of animals from that which would be observed in the absence of disturbance (Frid and Dill, 2002). With increasing use of the countryside for recreational activities, there is concern that human disturbance could negatively impact bird populations through, for example, influencing nest site choice (Lopez-Lopez *et al.*, 2006, Gonzalez *et al.*, 2006, Gavashelishvili and McGrady, 2006) or feeding areas (West *et al.*, 2002); causing detrimental physiological effects such as increased heart rate (Huppop 1995, Nimon *et. al.* 1996) or the secretion of stress hormones (Huppop & Gabrielsen 1998); and impacting on breeding success (Finney *et al.*, 2003, Yasue and Dearden, 2006).

Most studies are correlative, and relate population density, population size or demographic rates to measured disturbance levels. One problem with this approach is how to actually measure the

level of disturbance at a site. The most usual method is to count the frequency of events per unit time in a given area to provide a *disturbance event rate* relative to other sites. This is widely used and has been successful in that correlations have been found between aspects of breeding success and distribution and disturbance levels (Ruhlen *et al.*, 2003, Liley, 1999, Mallord, 2005). The advantage of this type of measurement is that, if sufficient representative samples are taken, it can provide accurate average levels of disturbance within the study period. However, the method usually involves prolonged periods of survey to obtain accurate mean levels of disturbance. Liley (1999) showed that disturbance varied temporally between weekends and weekdays and during school holidays, so it is important that sampling is representative and has good coverage of times of the day and days of the week. Furthermore, unless the disturbance occurs within a small area (Liley *et al.*, 2006) or exclusively on well used paths or tracks (Finney *et al.*, 2003) it can be difficult to measure the spatial distribution of disturbance at a site (Hill *et al.*, 1997) so as to include disturbance events over the entire area within which they might effect the birds. This method also requires that a zone of survey is established and that may require the definition of an arbitrary limit to observations. There is a danger of defining zones that included areas beyond the detection range of the animal or that are too small to incorporate all disturbance events of concern. Hence, disturbance event rates may be over- or underestimated compared with the biologically meaningful rates (Preisler *et al.*, 2005, Miller *et al.*, 2001).

To overcome or avoid some of these problems, correlates of disturbance have been used as proxies for direct measurements of event rates. Proxies include the distance to the nearest road, access points or area of human habitation, or the number or area of such features within a specified distance (e.g. Donazar *et al.*, 1993, Moran-Lopez *et al.*, 2006). The majority of these studies presume there is a correlation between the proxy and the disturbance, which may not always be true, and care needs to be taken when considering potential correlates as spurious results can emerge. For example, Moran-Lopez *et al.* (2006) showed that cinereous vultures *Aegypius monachus* showed a clear preference for selecting nest sites isolated from human dwellings and transport infrastructure and these were assumed to be surrogates for levels of human disturbance. However, as they acknowledge, the surrogates were also highly correlated with habitat variables such as slope, and vultures may be responding to these rather than disturbance. Hence, using proxies for disturbance increases the risk of spurious correlations. Furthermore, in the same paper, when looking within a smaller area, nest site preference was negatively related to distance to villages and areas of high human density. This counterintuitive

result was assumed to be a geographical artefact stemming from the simple assumption that the disturbance effect is only due to distance.

Where there are robust relationships between disturbance and static features such as roads or villages, results can be applied to the management of sites in relation to disturbance (Poirazidis *et al.*, 2004), but this approach has only been successful in a few studies where there are limited entry points into the reserve or country park. For example, Mallord (2005) found that disturbance on heavily used country park sites in Dorset was negatively correlated to the distance to the car park, with the majority of visitors travelling no further than 400m from their cars, and from this it was possible to predict the impacts of the creation of new car parks and paths on woodlark *Lullula arborea* use of breeding habitat. Similarly, on Thames Basin Heaths, Liley *et al.* (2006) found that the numbers of visitors was related to the amount of housing around a site and access point variables and recommended using the method to predict disturbance levels at unsurveyed sites or to predict changes in disturbance resulting from new housing developments.

Stone curlews *Burhinus oedicnemus* are considered to be vulnerable to human disturbance because they nest on the ground in open habitats and occur near some of the densest human populations in England. Furthermore, the CRoW Act has opened up their preferred lowland chalk grassland and heathland habitats to general access on foot, which could potentially mean elevated levels of disturbance near nest sites. At present most stone curlews in Wessex breed on specially created stone curlew plots, cultivated bare areas 1-2ha in size, which provide an alternative to short semi-natural chalk grassland and sparsely vegetated spring-sown arable crops, both of which are scarce in the region (Green *et al.*, 2000). Conservation programmes and agri-environment schemes exist to fund the creation of new nesting plots. Hence, if stone curlew behaviour is sensitive to disturbance around nest sites and this affects plot use, the ability to predict likely levels of disturbance near stone curlew plots is extremely valuable as it could greatly improve the placement of new habitat to maximise usage by stone curlews.

2.3 Aims of chapter

The aims of this chapter are to:

1. Describe the current average disturbance levels and regimes around stone curlew sites in the study area.
2. Model disturbance event rates as a function of potential disturbance correlates such as distance to villages and access points.

3. Establish if perceptions of disturbance event rates by people familiar with the sites are accurate.

2.4 Methods

Wessex, and in particular the area around Salisbury Plain (Figure 2.1), was chosen for this study of stone curlews and disturbance because it is exposed to various types of military training and recreational access. The population of stone curlews in this area has been studied by the RSPB since 1987. Therefore, historical information on distribution is available, most breeding attempts have been monitored and more than half of the adults are individually marked with colour rings applied when they were chicks.

2.4.1 Selection of study sites

In Wessex, specially created stone curlew plots have been significant in the recent population recovery (Figure 2.2). Between 1999 and 2005 (including the 2001 Foot and Mouth year) 48-60% of first nesting attempts each year were on specially created stone curlew plots (Figure 2.3). Plots are approximately the same size (1-2 ha) and their vegetation and substrate characteristics are managed to be broadly similar. Therefore, plots were ideal study units compared to arable field or chalk downland nesting sites where characteristics affecting their use by breeding stone curlews were much more variable. Each year around 250 artificial plots are managed on suitable soil types in Wiltshire, Hampshire, Berkshire and Oxfordshire specifically to provide habitat for nesting stone curlews. As part of the recovery project is to increase the range of the stone curlew from the current core centred on Salisbury Plain and Porton Down, plots may be in sites not yet colonised by the expanding population. I wished to select a subset of plots that were within the current core range of the stone curlew in Wessex, so that the failure of a plot to be used for breeding would be unlikely to be caused by the chance absence of potential colonists. I did this by calculating for each available plot in 2004 and 2005, the harmonic mean distance of the plot from all known breeding attempts in the years 2000, 2002 and 2003 combined. There were 227 breeding attempts (including first attempts and replacement clutches) in Wessex by stone curlews between 2000 and 2003 (excluding the 2001 foot and mouth year) (referred to here as *breeding attempts*). In 2004 and 2005 there 235 plots potentially available for breeding stone curlews through agri-environment schemes and other prescriptions (referred to here as *available plots*). To select the available plots closest to the core of the recent breeding range of stone curlew (as defined by the breeding attempts) I calculated the harmonic mean distance from each available plot to all breeding attempts in 2000, 2002 and 2003. Breeding attempts in the 2001 Foot and

Mouth epidemic year were excluded from this process as survey coverage was incomplete. The distance from each available plot to each breeding attempt was calculated using eastings and northings and Pythagoras' theorem. The mean of the reciprocals of these distances was then calculated for each available plot. The reciprocal of that mean is the harmonic mean distance for each available plot to all the breeding attempts in Wessex in 2000, 2002 and 2003. Available plots were then ranked according to their harmonic mean distance and those with the smallest values (i.e. those least isolated from the core of the recent breeding population) were selected for study using a cut off distance of approximately 1500 m to give the highest-ranked 75 plots. Plots within the boundaries of DSTL Porton Down were not used because the plots were not accessible to me during the breeding season whilst military operations were occurring and so measures of disturbance event rate were not obtainable. The harmonic mean distance variable was also used in many subsequent analyses and is referred to as *distance to core of population (m)*.

The distribution of the 75 plots selected using this method was centred on Salisbury Plain Training Area (SPTA). SPTA is split into three distinct areas: West, Centre and East ranges (Figure 2.4). The live firing range of SPTA West is at the extreme western edge of the stone curlew range and supports a maximum of three pairs annually. As a result of the peripheral location, the site selection procedure did not select any plots on SPTA West. SPTA Centre is also a live firing range with stone curlew plots distributed around the edge of the impact area. The plot selection procedure selected 14 plots on SPTA Centre. The final area of SPTA, SPTA East, is a 'dry' training area which means that no live firing takes place (except in one small section – see 2.4.2). As a result the area is open to recreation and I was able to have access at all times. Twenty-seven plots on SPTA East were selected using the method described, giving a total of 41 plots on SPTA. The majority of plots on SPTA are within semi-natural chalk grassland (90%). The remaining 34 plots were located off SPTA in surrounding farmland and are mostly within arable crops (71%) or semi-natural chalk grassland reversion schemes (29%). The extremes of the 75 plots formed a boundary approximately 24km by 21km (Figure 2.4) within which other breeding attempts were located (e.g. in arable fields or on disturbed ground).

The 75 plots were selected prior to the 2004 breeding season. As plots must be re-created for stone curlews before the breeding season each year I could not check that all had been managed until I started fieldwork in late February. In 2004, 69 of the plots were managed for stone curlews at some stage in the breeding season and in 2005 71 were managed. Sixty-seven of the plots were available as potential nesting sites in both years. In addition to plots, the tank driver

training area (DTA) on SPTA East provides a 30 ha area for stone curlews where vehicle disturbance of the sward has created suitable habitat. This site was surveyed in both years. Additionally, one other area of disturbed ground (1 ha) on SPTA East was created at the end of 2004 and available for breeding in 2005.

2.4.2 Stone curlew surveys

The RSPB Wessex Stone Curlew Recovery Project has surveyed the breeding population of stone curlews in Wessex since the mid 1980s. The recovery project has significantly contributed to increasing numbers of breeding stone curlews in the region, through nest protection measures and habitat creation (Figure 2.2). In each season, fieldworkers endeavour to locate all stone curlew breeding attempts in Oxfordshire, Berkshire, Hampshire and Wiltshire, monitor nests and provide protection where necessary. I worked alongside the Project team, taking over survey responsibility for my study area (Figure 2.4). All survey work was performed under a Wildlife and Countryside Act 1981 Schedule 1 Disturbance License issued by English Nature. Fieldwork on SPTA was carried out after a full MoD safety briefing and under the appropriate access permit.

Stone curlews return to the UK from wintering areas in mid-March. In 2004 and 2005, I started surveys for stone curlews at the beginning of March. Sites were visited for one hour every three days during the settlement period (20 March – 20 April – see section 2.3.1) when pairs were establishing territories and potentially moving between sites (Chapter 8). Visits occurred on all days of the week, including weekends. After 20 April, sites were visited every three to five days on a morning (08.00-12.00 BST), afternoon (12.00-17.00) and evening (17.00-21.00 or dark if earlier) rotation. In some areas, especially on SPTA, more than one site could be monitored at once, especially if no birds were present or if disturbance was absent or very infrequent.

There are two areas of SPTA where there is live firing during weekday daylight hours and some evenings and weekends. One (Bulford Ranges on SPTA East) is a 1km² exclusion zone for a live firing range and the two plots within the range can be assumed to have no disturbance from people or vehicles when red flags are flying. For the second area (SPTA Centre), of 14 plots, only two were so far into the red-flagged area that they could not be surveyed from beyond the flags. When I could not access these two sites I obtained data from MoD site users on approximate levels of activity during the designated hour, which was usually no activity or vehicular disturbance only.

During the 1-hour watches I surveyed for stone curlews from a stationary vehicle at a fixed position at least 300 m away, using a telescope. The long distance, use of a vehicle as a hide and using the same position for all surveys meant disturbance by me during surveys was minimal. The position of the vehicle was chosen to optimise the view of the stone curlew plot but also the surrounding area so that disturbance events could be monitored.

As the breeding plots are well defined and small (1-2 ha in most cases) it was possible to determine whether the plot was occupied or not by stone curlews by slowly scanning the whole area. At non-plot sites (DTA and cultivated fields), where the area to scan was larger and topography meant some areas were not visible, a tape recording of a stone curlew calling was very occasionally used to elicit a response from any birds present. This is a reliable method of checking for presence or absence as stone curlews will readily respond to other birds calling. This method was only used occasionally and after checking with a telescope first, because of a risk of effecting plot occupancy.

After locating stone curlews, the identity of ringed pairs was determined by reading individual colour rings, allowing birds' history to be established for analyses in subsequent chapters. I also attempted to determine which bird was the male and female in a pair. This is usually straightforward if both birds in a pair are seen side by side as the male has a more clearly defined wing bar (Green and Bowden, 1986).

Once birds were settled on breeding territories, visits continued to record the first signs of breeding. As both adults incubate eggs, breeding could be confirmed by a 'change-over' at the nest, where one bird relieves the other from incubation duties. Nests were then visited to record the number of eggs (Figure 2.5), and to weigh and measure the eggs to predict hatching date and also the date of the first egg based on calculations by R.E. Green (*pers. comm.*). Egg length and breadth were measured to 0.1 mm with dial calipers and mass was measured to 0.1 g with electronic scales. An eight figure grid reference was also taken and details of the nest site made to facilitate re-finding the nest to confirm hatching or failure. As incubation is continuous, shared equally between the male and female, progress and nest survival could be monitored from a distance by checking a bird was still sitting at the nest site. Hatching could usually be confirmed by seeing chicks with adults after hatching, but where birds moved after hatching, lost chicks immediately after hatching or where habitat changes made it difficult to see the area, hatching could be confirmed by the presence of small fragments (< 2 mm) of egg shell in the nest scrape

(Bealey *et al.*, 1999). If birds failed through predation at the egg stage any signs that predators left at the site were recorded (e.g. footprints, teeth marks on egg shell fragments). Chicks could be monitored by watching the site after hatching as it is unusual for the parent birds to take them off the plot and away from the nest site (Bealey *et al.*, 1999). Additionally, even if chicks themselves were not visible, the behaviour of the adult birds, through being particularly active during daylight, brooding chicks, carrying of food items to them or giving specific alarm calls when disturbed, could all be used to suggest chicks were present nearby.

Stone curlew chicks are large enough to be ringed approximately 14 days after hatching. At this stage they were located by one person observing the parent birds until the chicks appeared, and then watching the chicks with a telescope or fixing on the last known site of the chicks, whilst a second person walked to the site. Stone curlew chicks rely on their cryptic colouring to avoid detection and usually lie flat (Figure 2.6) rather than run from potential predators, therefore they could easily be located by the second person walking to the area the observer had last seen the chicks. Chicks were weighed to the nearest 1g using a Persola spring balance and bill length (tip to base of feathers) was recorded to the nearest 1mm with dial callipers (Figure 2.7). In addition, one metal BTO ring (size E) was fitted along with three Darvic colour rings in a unique combination (Figure 2.8). As stone curlews are long lived birds and spend much time ‘kneeling’ on stony surfaces in hot climates, the Darvic rings were glued to reduce the chance of rings being lost. Again, chick survival could be monitored remotely and fledging confirmed by the colour ringed individual being sighted away from the plot or in an autumn roost.

Stone curlews lay replacement clutches readily after egg and chick stage failures, with up to five nesting attempts recorded in a season (R.E. Green, *pers. comm.*). They can also fledge two broods in a season if breeding begins early enough and the habitat remains suitable, with the potential to fledge up to four chicks in one season. Replacements of failed nests or chicks and second broods were therefore also recorded.

2.4.3 Human disturbance surveys

On all suitable nesting plots, irrespective of whether stone curlews were using plots for breeding or not, routes followed by potential disturbance agents (PDAs) e.g. a walker, a walker plus a dog, or a vehicle, were mapped onto aerial photographs or maps during the 1-hour watches. PDAs were classed as people walking, soldiers, joggers, cyclists, horseriders, motorbikes, normal vehicles and armoured military vehicles (tanks). Data collection of PDA events commenced after

I had been in position for 15 minutes to allow any stone curlews present to settle from disturbance I may have caused when approaching my viewpoint. For each PDA event, the variables in Table 2.1 were recorded. The table includes some aspects of PDA events and stone curlew behavioural responses that are used in analyses in subsequent chapters.

2.4.4 Defining the area within which PDAs were visible to stone curlews from the plot

When considering how disturbance may affect stone curlews at nest sites, an important consideration is whether PDAs are visible to stone curlews from their location. In late February 2004 before plots were occupied by stone curlews, I measured a stone curlew's eye view from the centre of each plot by using a person at the plot to view the landscape from approximately 20 cm off the ground (the approximate mid height of a sitting/standing stone curlew) whilst a second person walked the main routes around the plot. Being in radio contact meant that when a person became visible or not visible to the observer the walker could take a GPS reading. This created a 'viewshed' from the stone curlew's point of view in which any disturbance events that occurred were visible. PDAs within this area were treated as potentially influencing the behaviour of the birds. It is thought that sounds produced by PDAs out of sight rarely caused behavioural responses because I did not observe obvious alert responses to sounds from sources out of view (E.C. Taylor *pers. obs.*).

2.4.5 Possible correlates of disturbance event rates

Possible correlates of disturbance event rates (Table 2.2) were measured from maps after the breeding season. These are variables that I expected might influence the rate at which disturbance events occurred and might be used to predict disturbance event rates at other sites. On SPTA there are two major access points to the eastern portion of the training area (SU 164461 and SU 149512). Although military activity can enter the training area at other points, these two tank crossings account for around 75% of vehicular access (E. Taylor *pers. obs.*). Tank crossings are often used by recreational users as places to park cars so this is included as a surrogate car park variable as well as a general access point variable. I do not consider distances to Public Rights of Way (PRoWs) or the density of PRoWs within a given area because I saw very little evidence of PRoWs being used, especially on grassland sites, and the majority of those that were used can also be classed as 'vehicle accessible tracks' and so are covered in the analysis.

2.4.6 Perceptions of disturbance event rates

I asked two stone curlew project members who had been involved in establishing plots to estimate how disturbed they thought the plots in my study area were. I provided them with a plot list and asked them to rank plots in terms of number of disturbance events per hour in a 300m radius of each plot. Additionally I asked them to state if they thought that the plot was not disturbed at all. Plots were then allocated to high, medium, low and zero disturbance categories. For each plot I then calculated the mean disturbance events per hour across two years of data collection and then applied the same ranking system to these values. The subtraction of the estimated rank from the actual rank then gave an indication of how accurate the estimated values were.

2.5 Data Analysis

2.5.1 Defining a settlement period

I defined a settlement period as being 20 March – 20 April. Figure 2.9 shows the cumulative proportion of pairs arriving on the site where they were first seen by date and the cumulative proportion of first egg dates. Arrival dates and first egg dates in 2004 and 2005 were combined and the mean proportion calculated. Approximately 10% of birds had arrived by 20 March, with 65% present by the end of the settlement period; and approximately 50% of pairs had their first egg date by 20 April.

2.5.2 Calculation of disturbance rates

Details of the mapped PDA events were used to calculate a crude *disturbance event rate* which was comparable between sites. Disturbance events are events that potentially alter behaviour, for example, walkers, dog walkers or vehicles. The use of disturbance event rates has been shown to be effective in describing the disturbance regime on sites (Ruhlen *et al.*, 2003, Liley, 1999, Mallord, 2005). The large number of observations at varying times of the day and week throughout the season are thought to give reasonable estimations of average disturbance event rates. Disturbance event rates may be over- or underestimated on the two plots on SPTA C where I could not have access during times of live firing. In these cases I relied on information from MoD users, which may not have been accurate.

For each site disturbance event rate was calculated as:

$$\text{Mean events per hour} = \frac{\text{the count of all PDA events observed in all observation periods}}{\text{total number of observation hours}}$$

To standardise between sites, a radius of 300m around the centre of the nest site was used as the maximum area within which disturbance events were counted. This variable is referred to in subsequent analyses as *season disturbance event rate* and includes all types of PDA event. I also calculated a second disturbance rate variable which described the mean disturbance rate during the time stone curlews were settling on breeding plots. This comprises PDA events observed between 20 March and 20 April only and is referred to as *settlement disturbance event rate*. This variable is used in analyses in later chapters.

PDA types can be classified in various ways and used to calculate event rates, as described above, for various aggregations of PDA types. In this chapter I consider the season and settlement rates of the following categories:

1. All PDA events per hour within 300m
2. Recreational PDA events per hour within 300m (including all civilian vehicles)
3. Recreational PDA events per hour within 300m (excluding civilian vehicles)
4. Walker and dogwalker events per hour within 300m
5. Civilian vehicle events per hour within 300m
6. Military PDA events (including normal military vehicles, tanks and soldiers on foot) per hour within 300m (on SPTA only)

In these analyses separate disturbance event rates were used for the 2004 and 2005 seasons and mean event rates were also used whereby the sum of the 2004 and 2005 event rates was averaged to create a mean disturbance event rate across both years

Univariate least squares linear regression was used to model season disturbance event rates in relation to possible disturbance correlates (Table 2.2) for 2004, 2005, and the mean for both years. Modelling was done separately considering all plots and SPTA plots only.

2.6 Results

2.6.1 Numbers, rates and types of PDA events

Across two years of data collection, 1417 disturbance events were observed on sites with stone curlew present. 823 of these were during six months in 2004 and 594 were during four months in 2005. This excludes experimental disturbance events I arranged (see Chapter 3). Twelve different types of PDA were observed, the commonest being vehicles and dog walkers which together accounted for 73% of all PDA events. In general, season disturbance event rate was low

across all sites (Table 2.3), with most sites experiencing less than 0.5 disturbance events per hour during the study periods (Table 2.3, Figure 2.10).

The 2005 study year was less disturbed than 2004 (Table 2.3). However, between the plots measured in both years there was a significant positive correlation in average disturbance event rate between the settlement periods (Figure 2.11) and between the whole seasons (Figure 2.12). Additionally, within years, the settlement disturbance event rate was significantly correlated with the season disturbance event rate (Figures 2.13 and 2.14).

2.6.2 Modelling the relationship between disturbance event rate and possible correlates

When all PDA types were considered for all plots in the study area, the season disturbance event rate was negatively correlated with the distance between the plot and the nearest vehicle accessible track in 2004 and for the mean values from both years (Table 2.4). The only significant relationship with recreational disturbance (including vehicles) was distance to the nearest track, and this relationship only occurred in 2004 (Table 2.5). However, there were no significant relationships between both recreational disturbance (excluding vehicles) and walker and dog walker disturbances and any of the potential correlates (Tables 2.6 and 2.7). There was a positive relationship between vehicle disturbance and distance to village in 2004 and overall, so that as distance from villages increased, disturbance from vehicles also increased (Table 2.8). Vehicular disturbance was also related negatively to distance to nearest track in 2004, 2005 and overall (Table 2.8).

On SPTA, mean disturbance (of any type) could be predicted from the distance to the nearest track (Table 2.9). However, neither recreational disturbance (including vehicles) nor recreational disturbance (excluding vehicles) was associated with any potential disturbance correlates (Table 2.10 and 2.11). The only significant relationship between walker and dog walker disturbance and potential correlates was that in 2005 the distance from track was positively related to disturbance (Table 2.12). Non military vehicle disturbance was positively related to distance from village and negatively related to distance to track in both years and overall (Table 2.13). Furthermore, military disturbance event rate was significantly negatively related to distance to track in 2005 and overall (Table 2.14). In 2005 military disturbance event rate was also positively associated with distance to training feature. There was also a relationship between disturbance and distance to a regularly used access point and disturbance was greater nearer to DTA (Table 2.14).

2.6.3 Perceptions of disturbance

Two people involved in plot placement were asked to rank a list of sites in terms of disturbance levels and specify any sites with zero disturbances. There was no significant correlation between observed rank and estimated rank (Spearman's rank $r = -0.071$, $N = 36$, $p = 0.68$). Figure 2.15 shows how the estimated ranks compared to the observed rankings. Approximately 30% of plots were assigned the correct level of disturbance, whilst 15% were underestimated and 55% were overestimated. In particular, there was overestimation of sites with zero disturbances as no sites in the study area were considered to be undisturbed.

2.7 Discussion

The majority of disturbance during the study was by vehicles and dogwalkers, which collectively accounted for 73% of PDA events. Compared to other studies (e.g. Liley, 1999, Liley *et al.*, 2006, Mallord, 2005, Taylor 2002), the disturbance event rate was very low despite all plots being near to villages, roads and potential access points. However, my sites differ from those in other studies because they are not within set recreation areas such as country parks and there are no *formal* access points such as car parks anywhere in my study area. For this reason it was thought that most of the disturbance originated from local villages, however, as discussed below this may not be the case. The low disturbance events rates observed is also a product of the habitat being artificially created specially for stone curlews and so there is consideration of disturbance levels when plots are created and usually sites with predicted low disturbance would be chosen.

Disturbance event rate was generally higher around SPTA plots because they are subject to military as well as recreational disturbance. SPTA is also an important archaeological and nature conservation site, and attracts a lot of birdwatchers, botanists and other specialist recreational users. The large networks of tank tracks make SPTA easily accessible to recreational PDAs, despite access on tracks not necessarily being permissible. The area of SPTA within my study area is 'open access' to recreation on PRoWs and in some areas more generally, for historic reasons. Restrictions to PRoWs are not observed by the public but there is tolerance of general access by land agents. Disturbance was lower in plots away from SPTA because many were in arable crops or on private land or have PRoWs further away.

Disturbance event rate in the 2005 study period was particularly low, which may be in part due to an increased effort by land agents to keep recreational disturbance low on SPTA and away from certain areas. Military disturbance was low during both years, possibly as a result of many units

being deployed to Iraq. In particular, there was infrequent use of the training area by soldiers on foot to what may be expected. Although 2004 was more disturbed than 2005, there was still a correlation in disturbance event rates and the highest disturbed plots in 2004 remained the highest disturbed plots in 2005. Similarly, although the month long settlement period was more disturbed in both years, the settlement disturbance event rates were correlated to levels for the rest of the season.

Some studies have shown that disturbance event rate can be modelled as a function of access points or the amount of urbanisation around a site (e.g. Liley, 1999, Liley, Jackson and Underhill-Day, 2006, Mallord 2003). The ability to do this would be extremely useful to stone curlew conservation if disturbance has an effect on behaviour, distribution or breeding success. For example, suitable areas for new habitat could be targeted. However, unfortunately my results show that there is no one clear model that can be used to predict disturbance around stone curlews plots in my study area.

As expected, general disturbance event rate, recreational disturbance event rate (including vehicles) and vehicle disturbance event rate was related to distance to the nearest vehicle accessible track. There was also a positive relationship between vehicle disturbance event rate and distance to village, indicating that vehicle users drive further to access more distance areas. This is supported by Liley, Jackson and Underhill-Day (2006) who report that people drove on average 15km to access Thames Basin Heaths. Recreational disturbance (excluding vehicles) and disturbance by walkers and dog walkers could not be modelled as a function of the potential disturbance correlates measured. Lack of association with any of the village variables indicates that people possibly do not walk from their homes to exercise, preferring possibly to use their car to drive further. This is in contrast to Liley, Jackson and Underhill-Day (2006) who found that recreational disturbance was related to the amount of housing around sites. However, their study sites were surrounded by a much greater density of housing and they considered 5km and 10km bands around site, whilst, in my study I only considered the area of housing within a 1km radius.

On SPTA plots, general disturbance and vehicle disturbance event rates was related to distance to tracks, as expected. However, walker and dog walker disturbance event rates were also related to tracks on SPTA. This may be because the potential of unexploded ordnance off the tracks discourages straying too far into the grassland. Again, there was a positive relationship between

vehicle disturbance and distance to village. Recreational disturbance event rate (including and excluding vehicles) on SPTA was not related to any potential disturbance correlates.

Military disturbance is sporadic and potentially less predictable than recreational disturbance, however, mean levels of military disturbance on SPTA were significantly related to distance to tracks. This is expected as much of military disturbance are convoys in transit on tracks going to other parts of the training area. Military disturbance event rate was significantly related to distance from training features, however, the relationship was positive so disturbance increased as distance from training features increased. It is thought that this is a product of most of the training features used as potential correlates in this study, being in the northern parts of SPTA East, whereas most military disturbance occurs in the southern portion. Military disturbance event rate was higher nearer to one of the two main access points onto the training area, but it was not related to access points in general, as a result of many access points being unsuitable for tanks. Finally, military disturbance event rate was higher on plots nearer to the tank driving area (DTA) because this is a military focal point on the Plain and large convoys have to pass stone curlew plots on their way to DTA. There was no relationship between military disturbance event rate and distance to nearest training camp. This is not surprising given that the origin of most military disturbances is unknown. The variable used was the straight line distance to the nearest camp but the disturbance may have come from any training camp within SPTA.

The disturbance rankings by land managers show that perceptions of disturbance at a site are not always accurate and in particular, disturbance appears to be over estimated. This could have serious consequences for management if decisions concerning new habitat are based on such perceptions. This is not a criticism of the current placement of plots as many other factors have to be incorporated into the decision and the measurement of disturbance is difficult. It is perhaps not surprising that perceptions of disturbance are not entirely accurate because the times field workers spend at plots are usually out of ‘normal’ recreational times, such as very early in the morning or late in the evening when stone curlews are most active. However, if disturbance is a problem to stone curlews, ways to improve estimation of disturbance levels is critical.

Where relationships exist between disturbance event rate and possible disturbance correlates, models may be used to predict the level of disturbance expected at current sites and future sites, and in the absence of other data this may be the only option. However, models are only really appropriate for vehicular and military disturbance, and can not predict recreational events. Other

potential disturbance correlates and surrogates for access can also be considered and measured such as the population living within other distance bands or the availability of alternative recreation sites (Liley *et al.*, 2006). The behaviour of people using sites such as SPTA warrants further study as does the establishment of the origin of recreational disturbance and in particular whether it is local or not. With changes in countryside access and building of new housing, particularly around Salisbury Plain, the ability to predict disturbance event rates is extremely valuable in the management of access and the placement of new habitat for stone curlews.

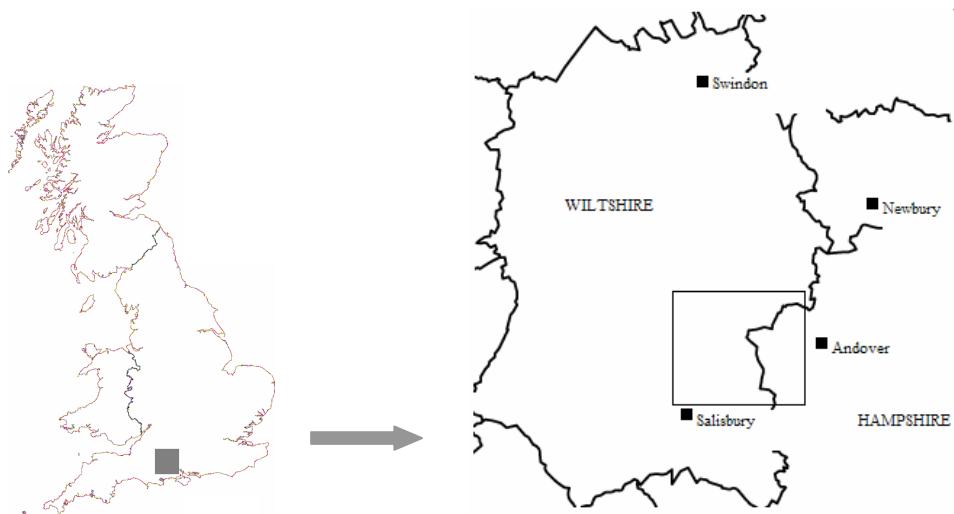


Figure 2.1. UK outline map showing the location of Wessex, and a close up of Wessex with the county names, location of main towns and approximate boundary of study area.

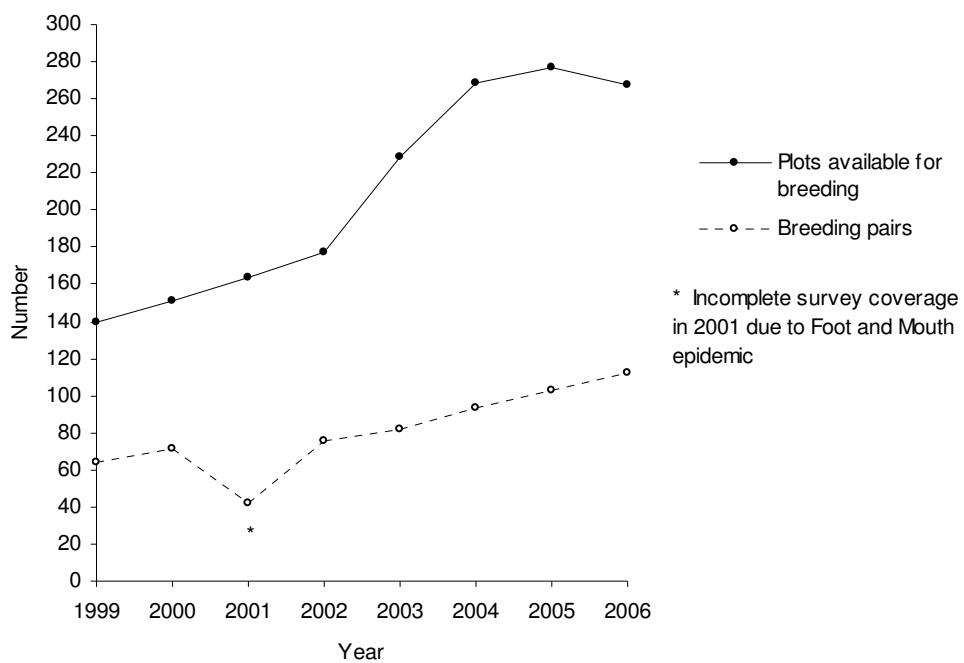


Figure 2.2. The number of breeding pairs of stone curlews in Wessex has steadily increased as the recovery programme addressed habitat loss through the creation of nesting plots and implemented nest protection measures.

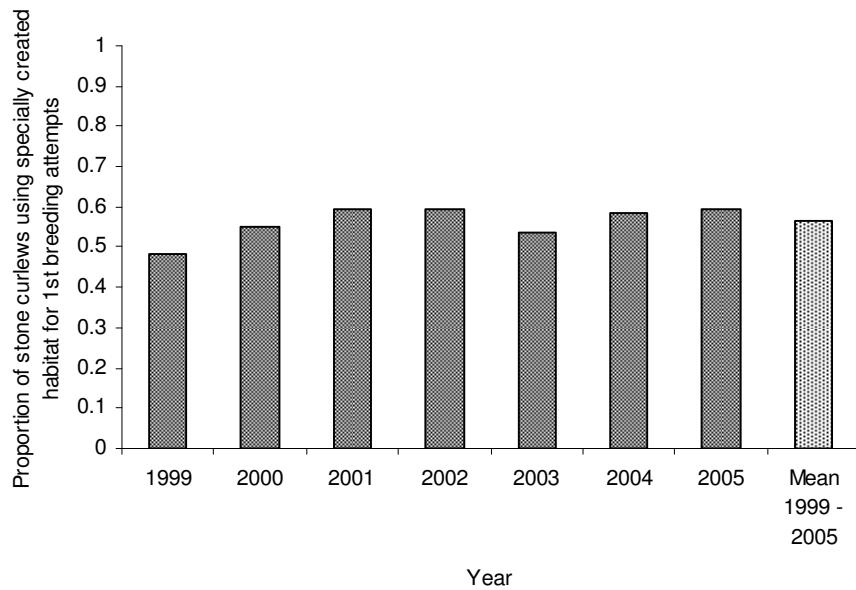


Figure 2.3. First breeding attempts on specially created stone curlew plots since 1999 as a proportion of total first nesting attempts in Wessex.



Figure 2.4. Aerial photograph (courtesy of Google Earth) of study area. Marked are the city of Salisbury and the routes of the main A roads and A303 trunk road. Also visible are the western, central and eastern grassland areas of Salisbury Plain (red circles) and Porton Down (blue circle). The approximate boundary of the survey area in this study (section 2.4.1) is shown as the yellow box.



Figure 2.5. Stone curlews lay eggs in a scrape in bare ground, often decorated with small stones, twigs or snail shells. Usually, two eggs are laid but one egg nests are also common and, more rarely, three.



Figure 2.6. When approached by potential predators (in this case a member of the Wessex stone curlew team) stone curlew chicks rely on their cryptic markings to avoid detection and usually lie flat and still. This chick is approximately 14 days old.



Figure 2.7. The bill length and weight of chicks are measured at day 14 after hatching.



Figure 2.8. All chicks are fitted with individual colour rings at day 14 or soon after. One BTO metal ring and three Darvic colour rings are fitted in a unique combination. The metal ring must always be fitted below the tarsus joint. A total of two rings can be fitted below the joint and one above the joint.

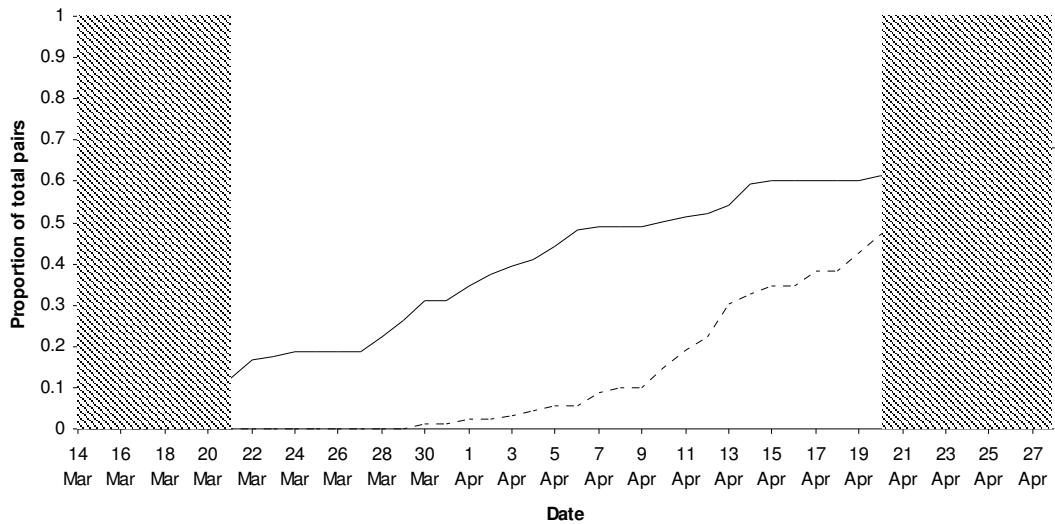


Figure 2.9. The cumulative proportion (mean of 2004 and 2005) of pairs of stone curlews arriving on the nesting sites where they were first detected in spring in relation to date (black line) and the cumulative proportion of 1st egg dates (dotted line). Shading shows the boundaries of the defined settlement period.

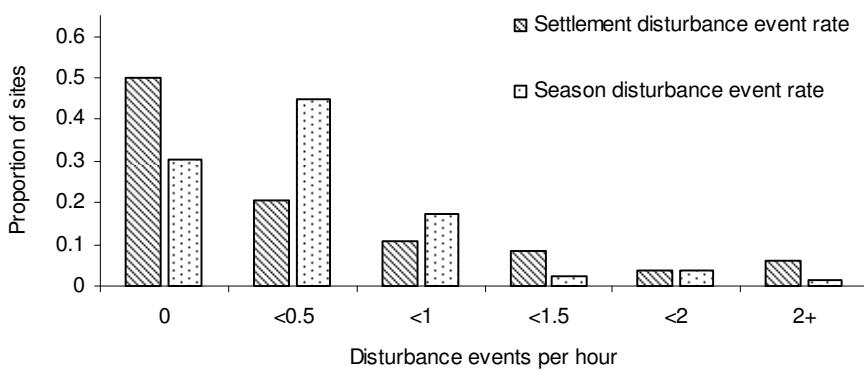
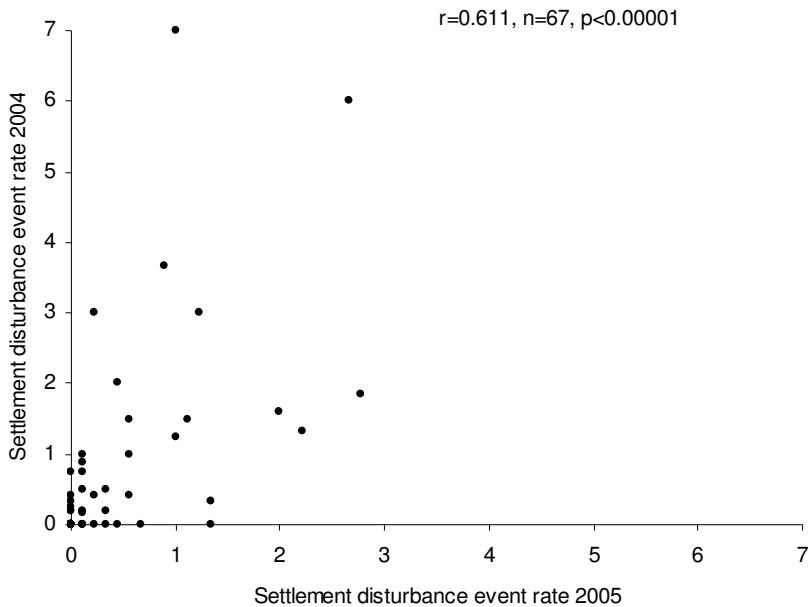


Figure 2.10. The frequency distribution of season and settlement disturbance event rates averaged for the two years 2004 and 2005.



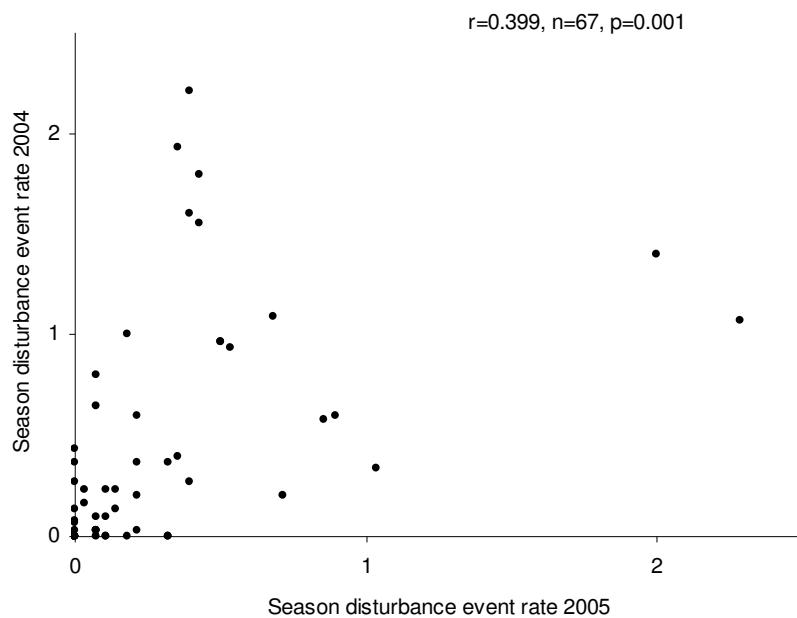


Figure 2.12. The relationship between season disturbance event rate in 2004 and 2005.

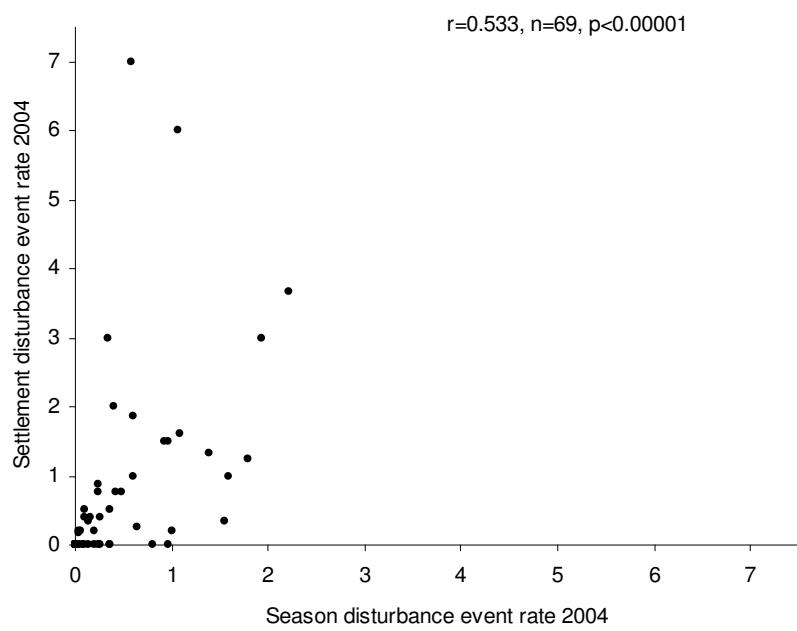


Figure 2.13. The relationship between settlement and season disturbance event rates in 2004.

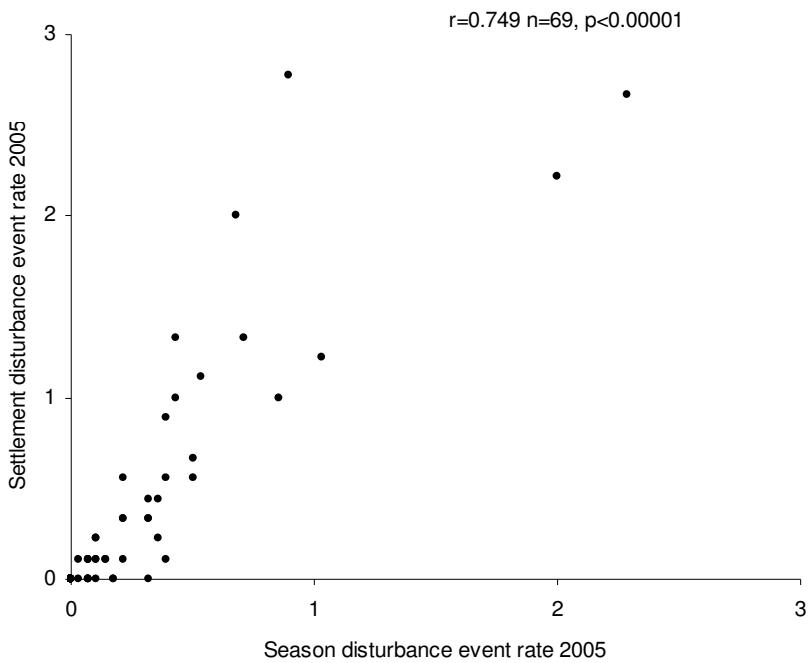


Figure 2.14. The relationship between settlement and season disturbance event rates in 2005.

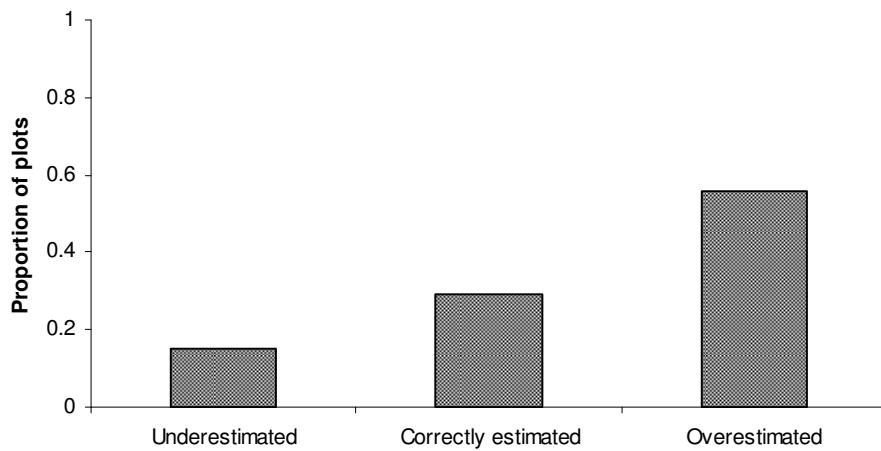


Figure 2.15. Proportion of plots underestimates, correctly estimated and over estimated in terms of disturbance by land mangers.

Table 2.1. Variables measured for each PDA event at sites with and without stone curlews.

Data recorded	Details
Position of stone curlew	Transferred onto aerial photo or map. For breeding birds the incubating or one with chicks was chosen. Where multiple birds were observed, or at different times of the season a bird was chosen at random.
Route of PDA visible to stone curlew	Transferred onto an aerial photo or map.
Start place	The point at which the PDA first becomes visible to the stone curlew
Type of PDA	People walking on foot (including soldiers), jogger, cyclist, horse rider, motorbike, normal vehicle, tank
Total agents	Number of different non dog components e.g. number of people, number of vehicles, number of joggers
Presence of dog	Presence of a dog with the PDA types described above
Julian date	Days from 1 January in each year
Year	The year during which the PDA event occurred – 2004 or 2005
Closest approach of PDA on route	The closest point the PDA got to the stone curlew or centre of stone curlew habitat on its entire route
Variables specific to sites with stone curlews present	
Stage of breeding	Settlement (pre-egg laying), egg, chick, post failure, roost or single bird.
Response of stone curlew to PDA (if any)	Classified as no response, alert, run, or fly
Position of PDA when stone curlew responds	Marked onto aerial photo or map
Distance between PDA and stone curlew at response	Measured for all response types (m)
Time taken for stone curlews displaced by PDA events to return to eggs or chicks	Measured for stone curlews at the egg and chick stages of breeding (seconds)

Table 2.2. Possible correlates of disturbance event rates.

Area	Measure	Description
All plots	Distance to nearest village	Straight line distance between plot and nearest village with >20 houses (m)
	Presence of village within 1km radius	Presence or absence of a village with >20 houses within a 1km radius of the centre of the plot
	Area of village within 1km radius	Total area of habitation within 1km radius of the centre of the plot (ha)
	Distance to nearest vehicle accessible track or road	Straight line distance between the plot and the nearest road or vehicle accessible track (m)
SPTA plots only	Distance to nearest tank crossing	Straight line distance between the plot and the nearest official tank crossing point onto SPTA (m)
	Distance to access point 1	Straight line distance between the plot and C crossing (SU 164461) (m). Tested in military disturbance model only.
	Distance to access point 2	Straight line distance between the plot and B crossing (SU 149512) (m). Tested in military disturbance model only.
	Distance to DTA	Straight line distance between the plot and tank driver training area (m). Tested in military disturbance model only.
	Distance to nearest training feature	Straight line distance between the plot and official MoD training feature (m). Tested in military disturbance model only.
	Distance to nearest MoD camp	Straight line distance between the plot and nearest MoD camp (Netheravon, Tidworth, Bulford, Larkhill) (m). Tested in military disturbance model only.

Table 2.3. Summary of season disturbance event rates for all sites measured in 2004, 2005 and in the study period combined.

Year	Minimum	Maximum	Mean	Median	Standard deviation
2004	0	3.21	0.44	0.13	0.66
2005	0	2.29	0.31	0.11	0.50
Combined	0	2.96	0.39	0.14	0.52

Table 2.4. Results of univariate linear regressions relating season disturbance event rates to possible correlate of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting the term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.0578	0.2085	0.0002	0.0001	$3.93_{1,68}$	0.051
	2005	0.1830	0.1627	0.0001	0.0001	$0.70_{1,71}$	0.40
	Mean	0.1073	0.1635	0.0002	0.0001	$3.53_{1,73}$	0.063
Presence of village within 1km radius	2004	0.3473	0.1121	-0.1328	0.1121	$1.42_{1,68}$	0.24
	2005	0.3029	0.0861	-0.0100	-.0861	$0.013_{1,71}$	0.90
	Mean	0.3348	0.0878	-0.0812	0.0878	$0.85_{1,73}$	0.35
Area of village within 1km radius	2004	0.4623	0.0833	-0.0166	0.0219	$0.57_{1,68}$	0.45
	2005	0.3171	0.0623	-0.0060	0.0167	$0.18_{1,71}$	0.72
	Mean	0.4090	0.0629	-0.0129	0.0171	$0.56_{1,73}$	0.45
Distance to vehicle accessible track	2004	0.7179	0.01345	-0.0005	0.0002	$6.17_{1,68}$	0.015
	2005	0.4622	0.1019	-0.0003	0.0002	$3.28_{1,71}$	0.074
	Mean	0.6325	0.0996	-0.0005	0.0002	$8.47_{1,73}$	0.0047

Table 2.5. Results of univariate linear regressions relating season recreational event rates (including vehicles) in the whole study area to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.1212	0.1637	0.0001	0.0001	$2.41_{1,68}$	0.12
	2005	0.2284	0.1219	0.00001	0.0001	$0.012_{1,72}$	0.91
	Mean	0.1705	0.1221	0.0001	0.0001	$1.35_{1,73}$	0.24
Presence of village within 1km radius	2004	0.2979	0.0874	-0.0833	0.0874	$0.90_{1,68}$	0.34
	2005	0.2629	0.0641	0.0299	0.0641	$0.21_{1,72}$	0.64
	Mean	0.2823	0.0649	-0.0286	0.0649	$0.19_{1,73}$	0.66
Area of village within 1km radius	2004	0.3679	0.0649	-0.0086	0.0171	$0.25_{1,68}$	0.61
	2005	0.2407	0.0465	0.0004	0.0125	$0.0011_{1,72}$	0.97
	Mean	0.3083	0.0464	-0.0044	0.0126	$0.12_{1,73}$	0.72
Distance to vehicle accessible track	2004	0.5332	0.1060	-0.0003	0.0002	$4.038_{1,68}$	0.048
	2005	0.2959	0.0773	-0.0001	0.0001	$0.731_{1,72}$	0.39
	Mean	0.4242	0.0755	-0.0002	0.0001	$3.80_{1,73}$	0.055

Table 2.6. Results of univariate linear regressions relating season recreational disturbance event rates (without vehicles) in the whole study area to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.1914	0.1064	0.00001	0.0001	0.090 _{1,68}	0.76
	2005	0.2169	0.0737	0.00001	0.00001	1.73 _{1,72}	0.19
	Mean	0.2055	0.0794	0.00001	0.00001	0.19 _{1,73}	0.65
Presence of village within 1km radius	2004	0.2020	0.0562	-0.0268	0.0562	0.22 _{1,68}	0.63
	2005	0.1590	0.0389	0.0446	0.0389	1.31 _{1,72}	0.25
	Mean	0.1796	0.0419	0.0098	0.0419	0.054 _{1,73}	0.81
Area of village within 1km radius	2004	0.2223	0.0415	-0.0009	0.0109	0.0074 _{1,68}	0.93
	2005	0.1207	0.0281	0.0050	0.0076	0.43 _{1,72}	0.51
	Mean	0.1700	0.0300	0.0022	0.0082	0.070 _{1,73}	0.79
Distance to vehicle accessible track	2004	0.2912	0.0690	-0.0001	0.0001	1.51 _{1,68}	0.22
	2005	0.1136	0.0474	0.00001	0.0001	0.10 _{1,72}	0.74
	Mean	0.2005	0.0498	-0.0001	0.0001	0.47 _{1,73}	0.49

Table 2.7. Results of univariate linear regressions relating season walker and dog walker disturbance event rates in the whole study area to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.1502	0.0737	0.00001	0.00001	0.028 _{1,68}	0.86
	2005	0.1224	0.0309	0.0454	0.0309	2.16 _{1,72}	0.14
	Mean	0.1311	0.0317	0.0258	0.0317	0.66 _{1,73}	0.41
Presence of village within 1km radius	2004	0.1416	0.0389	0.0042	0.0389	0.011 _{1,68}	0.91
	2005	0.1224	0.0309	0.0454	0.0309	2.16 _{1,72}	0.14
	Mean	0.1311	0.0317	0.0258	0.0317	0.66 _{1,73}	0.41
Area of village within 1km radius	2004	0.1354	0.0287	0.0027	0.0076	0.12 _{1,68}	0.72
	2005	0.0825	0.0224	0.0060	0.0060	0.96 _{1,72}	0.32
	Mean	0.1071	0.0227	0.0045	0.0062	0.52 _{1,73}	0.472
Distance to vehicle accessible track	2004	0.1586	0.0482	0.0001	0.0001	0.25 _{1,68}	0.61
	2005	0.0584	0.0376	0.0001	0.0001	0.99 _{1,72}	0.32
	Mean	0.1054	0.0380	0.0001	0.0001	0.047 _{1,73}	0.82

Table 2.8. Results of univariate linear regressions relating season vehicle disturbance event rates in the whole study area to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	-0.0703	0.0728	0.0001	0.00001	9.33 _{1,68}	0.0032
	2005	0.0107	0.0554	0.0001	0.00001	3.92 _{1,72}	0.05138
	Mean	-0.0350	0.0536	0.0001	0.00001	10.99_{1,73}	0.0014
Presence of village within 1km radius	2004	0.0959	0.0404	-0.0565	0.0404	1.95 _{1,68}	0.16
	2005	0.1030	0.0299	-0.0137	0.0299	0.21 _{1,72}	0.64
	Mean	0.1027	0.0300	-0.0384	0.0300	1.63 _{1,73}	0.20
Area of village within 1km radius	2004	0.1456	0.0301	-0.0077	0.0079	0.95 _{1,68}	0.33
	2005	0.1182	0.0216	-0.0045	0.0058	0.58 _{1,72}	0.44
	Mean	0.1383	0.0215	-0.0066	0.0058	1.28 _{1,73}	0.26
Distance to vehicle accessible track	2004	0.2420	0.0484	-0.0002	0.0001	7.007_{1,68}	0.010
	2005	0.1804	0.0349	-0.0001	0.0001	5.49_{1,72}	0.021
	Mean	0.2236	0.0336	-0.0002	0.0001	11.31_{1,73}	0.0012

Table 2.9. Results of univariate linear regressions relating season disturbance event rates on SPTA to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.2384	0.3525	0.0003	0.0002	2.247 _{1,35}	0.14
	2005	0.2129	0.2673	0.0001	0.0001	0.86 _{1,38}	0.35
	Mean	0.2218	0.2602	0.0002	0.0001	2.54 _{1,39}	0.11
Presence of village within 1km radius	2004	0.5390	0.2847	-0.2164	0.2847	0.57 _{1,35}	0.45
	2005	0.2519	0.2087	-0.2162	0.2087	1.072 _{1,38}	0.30
	Mean	0.4066	0.2089	-0.2275	0.2089	1.18 _{1,39}	0.28
Area of village within 1km radius	2004	0.7378	0.1320	-0.0125	0.0531	0.055 _{1,35}	0.81
	2005	0.4589	0.0931	-0.0294	0.0389	0.57 _{1,38}	0.45
	Mean	0.6213	0.0924	-0.0227	0.0391	0.33 _{1,39}	0.56
Distance to vehicle accessible track	2004	1.0757	0.2170	-0.0009	0.0004	3.70 _{1,35}	0.062
	2005	0.6065	0.1597	-0.0004	0.0003	1.48 _{1,38}	0.23
	Mean	0.8951	0.1493	-0.0007	0.0003	5.36_{1,39}	0.025
Distance to tank crossing	2004	0.6748	0.4051	0.0001	0.0002	0.10 _{1,32}	0.75
	2005	0.1733	0.3012	0.0002	0.0002	1.11 _{1,35}	0.29
	Mean	0.4391	0.2889	0.0001	0.0001	0.63 _{1,36}	0.43

Table 2.10. Results of univariate linear regressions relating season recreational disturbance event rates (including vehicles) on SPTA to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.2747	0.2749	0.0002	0.0001	$1.33_{1,35}$	0.25
	2005	0.2288	0.1826	0.00001	0.0001	$0.28_{1,38}$	0.59
	Mean	0.2498	0.1883	0.0001	0.0001	$1.22_{1,39}$	0.27
Presence of village within 1km radius	2004	0.4542	0.2200	-0.1316	0.2200	$0.358_{1,35}$	0.55
	2005	0.1856	0.1414	-0.1499	0.1414	$1.12_{1,38}$	0.29
	Mean	0.3191	0.1493	-0.1399	0.1493	$0.87_{1,39}$	0.35
Area of village within 1km radius	2004	0.5717	0.1017	-0.0002	0.0409	$0.000020_{1,35}$	0.99
	2005	0.3289	0.0631	-0.0197	0.0264	$0.56_{1,38}$	0.45
	Mean	0.4494	0.060	-0.0099	0.0279	$0.12_{1,39}$	0.72
Distance to vehicle accessible track	2004	0.7790	0.1705	-0.0005	0.0003	$2.186_{1,35}$	0.14
	2005	0.3292	0.1103	0.00001	0.0002	$0.0090_{1,38}$	0.92
	Mean	0.5594	0.1112	-0.0003	0.0002	$1.57_{1,39}$	0.21
Distance to tank crossing	2004	0.7857	0.3106	-0.0001	0.0002	$0.31_{1,32}$	0.58
	2005	0.2323	0.2063	0.0001	0.0001	$0.29_{1,35}$	0.59
	Mean	0.4960	0.2076	0.00001	0.0001	$0.010_{1,36}$	0.92

Table 2.11. Results of univariate linear regressions relating season recreational disturbance event rates (excluding vehicles) on SPTA to possible disturbance correlates. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model.

Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.3326	0.1754	0.00001	0.0001	$0.010_{1,35}$	0.92
	2005	0.2587	0.1102	0.00001	0.0001	$0.83_{1,38}$	0.36
	Mean	0.2982	0.1231	0.00001	0.0001	$0.17_{1,39}$	0.67
Presence of village within 1km radius	2004	0.2929	0.1380	-0.0651	0.1380	$0.22_{1,35}$	0.63
	2005	0.1034	0.0865	-0.0677	0.0865	$0.61_{1,38}$	0.43
	Mean	0.1931	0.0969	-0.0623	0.0969	$0.41_{1,39}$	0.52
Area of village within 1km radius	2004	0.3472	0.0637	0.0038	0.0256	$0.022_{1,35}$	0.88
	2005	0.1676	0.0385	-0.0078	0.0161	$0.23_{1,38}$	0.63
	Mean	0.2499	0.0426	-0.0014	0.0180	$0.0062_{1,39}$	0.93
Distance to vehicle accessible track	2004	0.3872	0.1098	-0.0001	0.0002	$0.17_{1,35}$	0.67
	2005	0.0815	0.0650	0.0002	0.0001	$2.38_{1,38}$	0.13
	Mean	0.2285	0.0730	0.0001	0.0002	$0.12_{1,39}$	0.73
Distance to tank crossing	2004	0.5489	0.1932	-0.0001	0.0001	$0.86_{1,32}$	0.36
	2005	0.1571	0.1259	0.00001	0.0001	$0.0097_{1,35}$	0.92
	Mean	0.3325	0.1352	0.00001	0.0001	$0.28_{1,36}$	0.59

Table 2.12. Results of univariate linear regressions relating season walker and dog walker disturbance event rates on SPTA to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	0.2088	0.1178	0.00002	0.0002	0.0000098 _{1,35}	0.99
	2005	0.2192	0.0875	-0.0001	0.00001	1.79 _{1,38}	0.18
	Mean	0.2138	0.0919	0.00001	0.00001	0.49 _{1,39}	0.48
Presence of village within 1km radius	2004	0.1714	0.0927	-0.0423	0.0927	0.20 _{1,35}	0.65
	2005	0.0658	0.0696	-0.0479	0.0696	0.47 _{1,38}	0.49
	Mean	0.1152	0.0727	-0.0417	0.0727	0.32 _{1,39}	0.56
Area of village within 1km radius	2004	0.2084	0.0428	0.0014	0.0172	0.0069 _{1,35}	0.93
	2005	0.1115	0.0310	-0.0059	0.0129	0.21 _{1,38}	0.64
	Mean	0.1536	0.0319	-0.0018	0.0135	0.017 _{1,39}	0.89
Distance to vehicle accessible track	2004	0.1744	0.0736	0.0001	0.0002	0.32 _{1,35}	0.56
	2005	0.0077	0.0501	0.0003	0.0002	6.025_{1,38}	0.018
	Mean	0.0860	0.0532	0.0002	0.0001	2.35 _{1,39}	0.13
Distance to tank crossing	2004	0.4093	0.1282	-0.0001	0.0001	2.26 _{1,32}	0.14
	2005	0.1669	0.1000	0.00001	0.0001	0.37 _{1,35}	0.54
	Mean	0.2771	0.007	-0.0001	0.0001	1.49 _{1,36}	0.22

Table 2.13. Results of univariate linear regressions relating season vehicle disturbance event rates on SPTA to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to nearest village	2004	-0.0579	0.1288	0.0001	0.0001	5.44_{1,35}	0.025
	2005	-0.0299	0.0857	0.0001	0.00001	5.34_{1,38}	0.026
	Mean	-0.0484	0.0852	0.0001	0.00001	9.31_{1,39}	0.0040
Presence of village within 1km radius	2004	0.1633	0.1087	-0.0665	0.1087	0.37 _{1,35}	0.54
	2005	0.0822	0.0704	-0.0822	0.0704	1.36 _{1,38}	0.24
	Mean	0.1260	0.0738	-0.0776	0.0738	1.10 _{1,39}	0.29
Area of village within 1km radius	2004	0.2245	0.0502	-0.0040	0.0202	0.038 _{1,35}	0.84
	2005	0.1613	0.0314	-0.0120	0.0131	0.83 _{1,38}	0.36
	Mean	0.1995	0.0326	-0.0085	0.0138	0.37 _{1,39}	0.54
Distance to vehicle accessible track	2004	0.3919	0.0796	-0.0004	0.0002	6.68_{1,35}	0.014
	2005	0.2476	0.0520	-0.0002	0.0001	4.542_{1,38}	0.039
	Mean	0.3309	0.0496	-0.0003	0.0001	11.00_{1,39}	0.0019
Distance to tank crossing	2004	0.2368	0.1568	0.00001	0.0001	0.0013 _{1,32}	0.97
	2005	0.0751	0.1011	0.0001	0.0001	0.95 _{1,35}	0.33
	Mean	0.1653	0.1026	0.00001	0.0001	0.24 _{1,36}	0.62

Table 2.14. Results of univariate linear regressions relating season military disturbance event rates on SPTA to possible correlates of disturbance. Shown are the coefficients of the terms in each model and the F value and P value from deleting each term from the model. Models are shown for 2004, 2005 and mean season disturbance event rates.

Predictor	Year	Intercept	SE	Slope	SE	F	P
Distance to vehicle accessible track	2004	0.3064	0.1068	-0.0004	0.0002	$2.72_{1,35}$	0.10
	2005	0.2773	0.0760	-0.0004	0.0002	5.84_{1,38}	0.020
	Mean	0.3358	0.0769	-0.0004	0.0002	7.21_{1,39}	0.010
Distance to tank crossing	2004	-0.1161	0.1803	0.0001	0.0001	$2.55_{1,36}$	0.11
	2005	-0.0296	0.1463	0.0001	0.0001	$1.37_{1,36}$	0.24
	Mean	-0.0569	0.1519	0.0001	0.0001	$2.71_{1,36}$	0.10
Distance to access point 1	2004	0.4445	0.1874	0.00001	0.00001	$2.62_{1,36}$	0.11
	2005	0.4538	0.1446	-0.0001	0.00001	5.468_{1,36}	0.025
	Mean	0.5787	0.1483	-0.0001	0.00001	8.015_{1,36}	0.0075
Distance to access point 2	2004	0.1604	0.1473	0.00001	0.00001	$0.0010_{1,36}$	0.97
	2005	0.0480	0.1167	0.00001	0.00001	$0.63_{1,36}$	0.43
	Mean	0.1464	0.1242	0.00001	0.0001	$0.08678_{1,36}$	0.77
Distance to DTA	2004	0.1800	0.1087	0.00001	0.00001	$0.34_{1,35}$	0.5619
	2005	0.4037	0.0849	0.00001	0.00001	14.32_{1,35}	0.00057
	Mean	0.4032	0.0884	0.00001	0.00001	9.91_{1,35}	0.0033
Distance to training feature	2004	0.1374	0.0968	0.00001	0.0001	$0.061_{1,36}$	0.80
	2005	-0.0086	0.0713	0.0001	0.00001	6.45_{1,36}	0.015
	Mean	0.0583	0.0776	0.0001	0.00001	$4.04_{1,36}$	0.051

3 The behavioural response of stone curlews to disturbance by human activities in the breeding season

3.1 Summary

Stone curlew behaviour in response to potential disturbance agents (PDAs) near nest sites was observed across several sites in two breeding seasons. Obvious changes in behaviour were recorded in response to 65% of the 1020 PDA events observed where stone curlews were present. The commonest response was to become alert, but 34% of PDA events evoked an active response (running or flying in response to the disturbance). Logistic regression modelling showed that the distance between the PDA at the closest approach distance was the most significant variable affecting whether or not a response occurred. However, the probability of an active response was also higher when the disturbance was by people on foot rather than motor vehicles. Furthermore, the presence of a dog with a person produced a greater probability of response. When response probability was modelled separately for vehicles and people on foot, models showed that for vehicles stone curlews were significantly more likely to respond to events occurring away from the most frequently used route at a site and where PDAs came closer to nesting sites. For people on foot, in addition to the closest approach variable, the probability of an active response was increased by the presence of a dog, at stages of the breeding cycle, and on infrequently used routes.

The mean distance at which stone curlews first showed alert and active responses to a PDA event was 242 m and 185 m respectively. These distances are large compared with those for most other bird species. Furthermore, stone curlews reacted at significantly shorter distances for vehicles compared to people on foot and with dogs. After disturbance events that produced active responses, the mean time taken for stone curlews to return to nests or chicks was 4.86 minutes. This time was not correlated with any of the measured variables.

Whilst these analyses give first descriptions of how stone curlews respond to disturbance, the usefulness of the results is limited and management of access based on this approach would be difficult, costly and impractical.

3.2 Introduction

The impact of human disturbance on animal populations has long been studied in conservation biology (Stalmaster and Newman, 1978, Miller *et al.*, 1998, Bélanger and Bédard, 1989, Hockin *et al.*, 1992, Gill *et al.*, 2001, West *et al.*, 2002, Beale and Monaghan, 2004, Gonzalez *et al.*, 2006), because of a perceived conflict between wildlife and human use of the countryside (Béchet *et al.*, 2004). Since the 1970s, the number of scientific papers published each year concerning the effects of human disturbance has increased steadily (Hill *et al.*, 1997) and in the 10 years between 1988 and 1997 Gill and Sutherland (2001) reported that 308 papers with ‘human disturbance’ as a keyword were listed on the BIDS reference library.

Whilst disturbance studies may be common, they vary greatly in their subjects, objectives and conclusions. The coverage of major habitat types and species is patchy and uneven and many disturbance papers contain speculative conclusions and may be misleading (Sidaway, 1990). In particular, it is rarely the case that these studies provide clear evidence that human disturbance limits population size or causes population decline. One reason for this is that most disturbance studies are made at a restricted scale in terms of the proportion of the species’ geographical range and the proportion of the population studied. Hence, they are not easily interpreted for the species concerned, and so can not easily be extrapolated to the population level or translated to other species and habitats. Despite this, the two key texts documenting bird populations in the UK (Batten *et al.*, 1990) and Europe (Tucker and Heath 1994) report ‘human disturbance’ as being a *potential* factor in population declines of a number of species e.g. red-throated diver *Gavia stellata*, black kite *Milvus migrans*, Kentish plover *Charadrius alexandrinus*, nightjar *Caprimulgus europaeus* and chough *Pyrrhocorax pyrrhocorax*. Specifically, 42% of Red Data Birds in the UK are classified as at risk from disturbance (Batten *et al.*, 1990) and 27% of the Species of European Conservation Concern (Tucker and Heath 1994). Furthermore, Pritchard *et al.* (1992) report that 49% of IBAs in Scotland, 76% in England, and 71% in Wales are affected to some extent by human disturbance.

Disturbance can be defined as a deviation in an animal’s behaviour from patterns occurring without human influence (Frid and Dill, 2002). Studies of observations of flight distances and other responses to disturbance are common (Burger 1981, 1991, 1994, Yalden and Yalden, 1990, Yalden 1992, Fitzpatrick and Bouchez 1998, Lafferty, 2001). This type of change in behaviour is the simplest to study as there is usually a visible response to the disturbance event. Responses to disturbance and flight distances are often used to manage disturbance levels at a site by

determining exclusion zones and set back distances in which disturbance is limited or excluded (e.g Richardson and Miller, 1997, Ronconi and St. Clair, 2002).

However, changes in behaviour as a result of human disturbance can also affect habitat use or distribution (Marsden, 2000, Evans and Day, 2001; Pfister *et al.*, 1992; van der Zande, 1984, Fernandez-Juricic and Telleria, 2000); and variation in breeding success (see review Hockin *et al.*, 1992). Mechanisms that underlie effects of disturbance on breeding success include attraction of predators (Gutzwiller *et al.*, 2002; Jokimaki and Huhta, 2000), avoidance by predators of areas used by people (Miller and Hobbs, 2000), increased risk of predation or breeding failure if birds are kept away from the nest (Verhulst *et al.*, 2001, Giese, 1996) and interference with foraging and the amount of parental care given (Fernandez and Azkona, 1993; Bautista *et al.*, 2004).

Whilst caution should be taken concerning the interpretation of behavioural responses to disturbance (Gill *et al.*, 2001), they remain the first measure of a species' sensitivity to human activity. Furthermore, although they may not reflect the population impact of disturbance they can be useful in certain management situations (Blumstein *et al.* 2005).

Given its vulnerable population status and the fact that the majority of favoured breeding habitat is open access land designated under CRow, an assessment of how sensitive stone curlew behaviour is in response to disturbance was required. Observations of behaviour in relation to disturbance have not been systematically collected for stone curlews. There is also an absence of other studies on related species in similar habitat. Therefore, in this chapter I aim to give a first assessment of stone curlew behaviour in response to human disturbance.

3.3 Aims of chapter

The aims of this chapter are to describe:

- 1) The types and frequencies of responses to PDAs by stone curlews;
- 2) Relationships between the probability of a response occurring and explanatory variables;
- 3) Distance between the stone curlew and PDA when different responses are observed;
- 4) Relationships between response distances and other explanatory variables;
- 5) Times taken for stone curlews to return to eggs or chicks after disturbance
- 6) Relationships between times taken to return and explanatory variables.

3.4 Methods

Study sites were selected according to the method described in section 2.4.1. Stone curlew and disturbance surveys were conducted using the methods described in sections 2.4.2 and 2.4.3.

3.4.1 Measuring behavioural responses to disturbance

Routes followed by potential disturbance agents (PDAs) e.g. a walker, a walker plus a dog, or a vehicle, were mapped onto aerial photographs or maps during the 1-hour watches. The variables in Table 2.1 were recorded for each observed PDA event. Data collection commenced after I had been in position for 15 minutes to allow any stone curlew present to settle from any disturbance I may have caused in driving to my vantage point.

At sites where stone curlews were present, a focal bird was also watched simultaneously and changes in behaviour in response to the PDA were recorded. If a pair was breeding, the focal bird was the one incubating eggs or nearest the chicks. For birds with no breeding attempt in progress, an individual was selected at random. For each PDA event, the variables in Table 2.1 were recorded.

Behavioural responses to disturbance were recorded at 41 nesting plots and six other sites. The additional sites were four areas (1-50 ha) on Salisbury Plain where disruption of the sward by vehicular disturbance has provided suitable nesting habitat, a 1 ha game strip sown with maize and a 2 ha area of set-aside farmland. The observations involved 40 different pairs of stone curlews.

3.4.3 Experimental disturbance events

To increase the number of incidents of PDAs on infrequently used routes and on sites without disturbance, a small number of experimental disturbances were performed at 28 sites (mostly on SPTA). In 2004 I carried out 112 experimental disturbances (78 by a walker, 24 by a walker with a dog, 10 by a jogger) on 24 sites (mean additional disturbance of 4.67 events per site in whole season). In 2005 there were 94 experimental events (56 by a walker, 27 by a walker with a dog, 11 by a jogger) on 15 sites (mean additional disturbance of 6.27 events per site in whole season). No sites were experimentally disturbed more than once in a given week.

The protocol for recording responses to experimental disturbance followed similar methods to the incidental disturbance events. The agent was briefed beforehand as to the route that should be

followed and supplied with a walkie-talkie radio and a GPS. I then dropped off the agent at the start point of the route where they were not visible to the stone curlew and parked at my usual vantage point. After waiting 15 minutes for birds to settle from any disturbance caused during this time, I instructed the agent to begin walking or jogging. If I observed a response from the stone curlew, I asked the agent for the 12 figure grid reference and recorded the variables in Table 2.1. The agent then carried on along the route until out of sight. Any subsequent responses by the stone curlew to the agent were also recorded.

3.4.4 Aspects of a behavioural response

In this chapter I consider three aspects of stone curlew behaviour in response to and after PDA events:

- Whether or not a stone curlew responded to a PDA event and the type of response shown.
- The distance between PDA and the stone curlew at point of response.
- The time taken for the stone curlew to return to the nest or brood after running or flying away.

In most of the analyses I have analysed two main types of response to PDA events: becoming alert to a PDA and running or flying away. I call the latter active responses.

a) Alert responses

Alert responses were considered to have occurred when an obvious change in behaviour was observed, but the bird remained at or close to its original position. The stone curlew usually stretches its neck or stands up (if initially sitting) or crouches (if initially standing) as the first visible response to disturbance by a predator or PDA (E.C. Taylor and R.E. Green *pers. obs.*). After standing the bird sometimes bobs its head up and down. Standing, neck stretching and head bobbing may improve the information the bird has about the PDA by giving it a better view. Sitting may increase the bird's concealment if its initial view of the PDA was already adequate. I refer to these aspects of stone curlew behaviour as showing an *alert response*. An alert response may represent the beginning of the decision process the stone curlew must go through to decide whether to remain on a plot or leave by running or flying. The alert response and its associated distance has been discussed by Fernández-Juricic *et al.* (2001) as being the most appropriate response to measure if trying to implement appropriate disturbance management solutions because it is more conservative than flight initiation distance. There are no obvious large direct

costs to the bird of an alert response, although stress levels, heart rate and energy consumption may well rise.

b) Active responses

Active responses were considered to have occurred when the bird began running or flying from its initial location in response to a PDA. Stone curlews may run or fly as a first response, or after becoming alert, or they may run and then later fly. Analogous with Flight Initiation Distance (FID) or flee distance in the disturbance literature, this response represents the tipping of the balance between the cost and benefit of remaining in position with an approaching disturbance stimuli. At the active response point the stone curlew has decided the risk is too great and responds by actively removing itself from the area. I have combined running and flying to make one active response because for stone curlews the result is similar. The active response was taken to have occurred when whichever response, running or flying, happened first. Stone curlews have been observed running long distances in preference to flying (E. Taylor pers. obs.). Their camouflaged plumage may allow them to do this without a human observer or predator necessarily noticing.

It is likely, although not certain without physiological testing, that active responses are more costly to the stone curlew than alert responses in terms of energy loss and stress. They, and the movement back to the nest or chicks, are probably also more conspicuous to predators and may therefore reduce breeding success. Active responses also remove the bird from the nest site, leaving eggs or chicks exposed to predators or thermal stress. Furthermore, running and flying are not usual activities during daylight for stone curlews and so elevation of active response rates beyond a background level represents a deviation in normal behaviour.

3.5 Data analysis

Univariate non-parametric tests were used to compare PDA events where a response was observed and not observed. I then used logistic regression to model the probability of a response being observed to the PDA events in relation to the variables measured in Table 2.1. These variables are further described in Table 3.1. The models were fitted using a logit-link function with a binomial error structure. Minimal adequate models (MAMs) were selected by backwards stepwise elimination, with variables deleted if their inclusion did not significantly decrease residual deviance (Crawley, 2002). Differences in response distance and time taken to return to eggs and chicks were tested with univariate tests.

3.6 Results

3.6.1 Summary of PDA events at sites where stone curlews were present

In addition to 206 experimental disturbances, 814 PDA events were observed at sites with stone curlews present over two years of data collection. Eleven types of PDA were recorded at sites with stone curlews (Figure 3.1) but the majority were vehicles, dog walkers or walkers, which collectively accounted for 76% of PDAs.

3.6.2 How do stone curlews respond to disturbance?

Stone curlews showed a response to 666 (65%) of the 1020 PDAs. The first responses and all responses, as proportions of total events are shown in Table 3.2 a and b. Almost 50% of PDA events caused an alert response as a first response and 17% caused an active response as a first response (Table 3.2a). 34% of PDA events caused an active response either as a first response or after first causing an alert response (Table 3.2b).

According to univariate nonparametric tests comparing PDA events with and without observed responses, stone curlews were significantly more likely to respond to disturbance if it was on an infrequently used route (Table 3.3). There were significantly less responses observed at the settlement stage compared to the egg stage ($\chi^2=13.33$, df=1, p= 0.0003) and chick stage ($\chi^2=7.96$, df=1, p=0.0048); and less responses at the roost stage than egg ($\chi^2=7.09$, df=1, p=0.0078) and chick ($\chi^2=5.79$, df=1, p=0.0161). There were also significant differences between disturbance types. Figure 3.2 shows the proportion of events where an active and alert response was observed for each PDA type. Stone curlews were more likely to respond to events involving walkers or dog walkers than vehicles ($\chi^2=300.45$, df=1, p<0.0001).

PDA events that started further from a stone curlew were less likely to produce a response, as were routes that came less close (Figure 3.3). However there were no differences in season disturbance event rate or date between those PDA events that caused a response and those that did not, and response was not associated with year (Table 3.3).

3.6.3 Modelling the probability of a response to a PDA event

I used logistic regression to model the probability of a response being observed to a given PDA event in relation to the variables measured in Table 2.1. Table 3.1 shows the candidate variables entered into models.

I carried out separate analyses for the two responses described in section 3.4.4:

1. Stone curlews showing an *alert response* to a PDA event (n=494/1020)
2. Stone curlews showing an *active response* (running or flying) to a PDA event (n=348/1020)

I first combined all data and produced MAMs to describe the probability of a response to any PDA event (section 3.6.3a) and then I split PDA types into vehicles (section 3.6.3b) and people walking on foot (section 3.6.3c).

a MAMs to describe the probability of a stone curlew showing a response to any PDA event

The MAMs to describe the probability of both an active and alert response to any PDA event included almost all of the candidate explanatory variables (Tables 3.4 and 3.5). The model fit of the closest approach distance alone for active and alert responses are shown in Figure 3.4.

b MAMs to describe the probability of a stone curlew showing a response to vehicle PDA events

When vehicle PDA types were considered separately, the MAM for alert responses included closest approach, disturbance type and the group size (Table 3.6). The MAM to describe the probability of an active response to a vehicle PDA event included the closest approach distance and the route. The probability of an active response increased as vehicles came closer and were on an infrequently used route (Tables 3.7). The model fit of the closest approach distance alone for active and alert responses are shown in Figure 3.5.

c MAMs to describe the probability of a stone curlew showing a response to people walking on foot PDA events

When people walking on foot were considered separately, the MAM describing an alert response included year, presence of a dog, closest approach and also the start distance (Table 3.8). The MAM describing an active response included the closest approach, route, presence of a dog, stage of breeding and group size (Table 3.9). Figure 3.6 shows the probability of active and alert responses to people on foot PDA events in relation to closest approach distance alone.

3.6.4 At what distances do stone curlews respond to disturbance?

There were significant differences in the average response distance among the different response types (Kruskal-Wallis $\chi^2=73.94$, df=3, p=<0.0001). An alert response occurred at significantly

larger mean distances than running (Mann Whitney $U=56760.0$, $df=785$, $p<0.0001$), flying (Mann Whitney $U=6732.0$, $df=551$, $p<0.0001$) or the two active responses combined (Mann Whitney $U=61738.5$, $df=827$, $p<0.0001$). Running responses occurred at significantly larger mean distances than flying (Mann Whitney $U=5198.5$, $df=347$, $p<0.0001$). The mean distances stone curlews showed different responses to disturbance are shown in Table 3.10.

There were no significant difference in response distance between stages of breeding for alert response (Kruskal-Wallis $\chi^2=3.047$, $df=4,493$, $p=0.550$), run response (Kruskal-Wallis $\chi^2=7.685$, $df=429$, $p=0.104$), fly response (Kruskal-Wallis $\chi^2=5.589$, $df=455$, $p=0.232$) or for active responses (Kruskal-Wallis $\chi^2=5.912$, $df=433$, $p=0.206$).

There were significant differences in response distances between disturbance types (Figure 3.7). Stone curlews responded to vehicles at significantly closer distances than walkers (Mann Whitney $U=8207.0$, $df=297$, $p=0.001$), dog walkers (Mann Whitney $U=10189.0$, $df=337$, $p=0.002$), and tanks (Mann Whitney $U=1542.5$, $df=152$, $p=0.010$) (Figure 3.7)

There were no significant differences between response distances on frequently and infrequently used routes (Mann Whitney $U=35561.5$, $df=66$, $p=0.197$). At a site level, there were no correlations between the mean response distance at a site for any disturbance type and the season disturbance event rate recorded at that site ($r=-0.172$, $n=40$, $p=0.289$).

There were strong positive correlations between response distance and start distance and closest approach distance (Table 3.11). However, these correlations are difficult to interpret because some of the correlation is an artefact because response distance can only be less than the start distance and must be greater than the closest approach distance.

3.6.5 Time taken for stone curlews to return to eggs and chicks after active responses

The mean time to return to nests or chicks after the 253 PDA events at these stages which caused a stone curlew to show an active response was 4.86 minutes (SD 2.92) (Figure 3.8). The minimum time was 0.20 minutes and maximum 17.40 minutes.

The time taken to return to nests or chicks was not correlated with response distance ($r=0.069$, $n=253$, 0.272), start distance ($r=0.028$, $n=253$, $p=0.653$), closest approach ($r=0.068$, $n=253$, $p=0.283$), or the season disturbance event rate recorded at the site ($r=-0.079$, $n=244$, $p=0.217$).

There was also no significant difference in time to return to nest or chicks between years (Mann Whitney U=6482.5, df=252, p=0.584), whether the PDA was on frequently used route or not (Mann Whitney U=6441.5, df=252, p=0.475), between the two breeding stages (egg and chicks) (Mann Whitney U=5970.5, df=252, p=0.348), between running and flying responses (Mann Whitney U=3546.5, df=252, p=0.831), or with disturbance type (Kruskal-Wallis $\chi^2=10.861$, df=10, 252, p=0.368).

3.7 Discussion

Stone curlews responded to 65% of PDA events observed in the study period. The most frequent response was to become alert to the disturbance, and over a third produced an active response. A number of studies have shown that birds can detect threats without necessarily expressing obvious alarm (Blumstein *et al.*, 2003, Gonzalez *et al* 2006). As a result, an alert response may not be perceived by the observer until the disturbance is very near the nest sites and a flight response is then observed. For these reasons, the difficulties in measuring an alert response, and the possibility of alert responses being less costly to stone curlews, I concentrate most of this discussion on the active response.

The probability of an active response increased sharply at distances less than 500m from the stone curlew. Comparative results are shown by Gonzalez *et al.* (2006) and Arroyo and Razin (2006). In the Gonzalez *et al* (2006) study imperial eagles *Aquila adalberti* showed increasing probabilities of flight and alert responses when disturbance occurred at distances less than 800m from the a nest site and probabilities rose sharply when activities were less than 450m away. In my study, when all PDA types are considered together, the MAM describing the probability of an active response includes most of the candidate variables. Disturbance type in particular was highly significant in the MAM and, as in common with other studies, there was a significantly larger effect of people on foot than vehicles (e.g. Gonzalez *et al.*, 2006; Richardson and Miller, 1997). It was therefore sensible to split the PDA types into two groups: vehicles and people on foot.

Stone curlews were significantly more likely to respond actively to vehicle PDA types if the PDA approached closer. The probability of a response rose sharply when the vehicle PDA approached closer than 400m which was similar to that found by Gonzalez *et al.* (2006). Furthermore, there were lowered probabilities of responding to PDA events on regularly used routes, possibly

suggesting some habituation or tolerance to disturbance in expected locations, as has been found in a number of other studies (Burger and Gochfield, 1983, Ikuta and Blumstein, 2003).

The MAMs describing a response by people walking on foot were more complex than for vehicles. The probability of an active response rose sharply when the PDA came closer than 600m to the stone curlew. As found in other studies, an infrequently used route caused a higher probability of a response which may be associated with habituation (Burger and Gochfield, 1983, Ikuta and Blumstein, 2003). The presence of a dog with the person caused a greater probability of response (Burger, 1981; Yalden and Yalden, 1990; Lord *et al.*, 2001), as did larger group sizes of people (Beale and Monaghan, 2004, Dill, 1974). Probabilities differed between different stages of the breeding cycle (Yalden and Yalden, 1989, Yalden, 1992), with responses occurring in a higher proportion of events at the egg and chick stages.

For stone curlews that responded to PDA events, the distance between the PDA and the bird when the response was observed was greater for alert than active responses. Alert responses were observed at a mean distance of 242 m between the PDA and the birds, and active responses were observed at a mean of 185 m. These distances appear to be substantially larger than for other wader species in the disturbance literature. Flemming *et al.* (1988) reports that piping plovers *Chararius melanotos* flush from nests at 40 m. Yalden and Yalden (1990) recorded that golden plover *Pluvialis apricaria* alarm called (surrogate for alert response) to anyone within 200 m during the chick stage but approaches could come within 10 m of incubating adults before they took flight. Additionally, nesting waterbirds, including waders, in Florida were observed to flush from nests at distances less than 30 m (Rodgers and Smith, 1995). The mean flight distances observed by stone curlews are more similar to those of birds of prey, rather than other wader species. For example, the average alert response distance recorded in Spanish imperial eagles was 252 m +/- 115 m (range 50-580) and the average flight distance was 261 m +/- 191 m (range 1-1000) (González *et al.*, 2006).

Many wader disturbance studies showing small response distances are post breeding (e.g. Ikuta and Blumstein 2003, Rodgers and Schwikert, 2002) or during the winter (e.g. Stillman and Goss-Custard, 2002) and may not be directly comparable to responses observed during the breeding season, however, even the response distance at the roost stage for stone curlews was large compared to much of the wader response distances that are reported in the literature. Stone curlews are large waders (adults weigh in excess of 500g) and it has also been reported that larger

species are less tolerant to disturbance and show greater response distances (Cooke, 1980, Humphrey *et al.*, 1987, Skagen *et al.* 1991, Holmes *et al.*, 1993). However, the species considered in these studies also often approach PDAs and attempt to drive them away, give distraction displays or alarm calls. It is thought that small wader species are less likely to do this because they are unable to intimidate PDAs because of their small size. Stone curlews do not give persistent alarm calls during the breeding season and do not attempt to drive away the PDA types considered in my study, although they do attempt to drive away stoats and livestock. Hence, the response to PDAs of stone curlews cannot be considered to be similar to that of most other large waders. Alternatively, it is possible that smaller species react later to conserve energy (Holmes *et al.*, 1993) or larger species may have better perceptual ranges related to the increased visual acuity of larger species (Kiltie, 2000) enabling individuals to detect and react to human approaches at greater distances. It is also possible that the sparse vegetation and open landscape of stone curlew habitat allows PDAs to be detected at greater distances than for birds nesting in taller vegetation or with a restricted viewshed, and therefore longer response distances are observed.

Response distance varied with PDA type, with dog walkers producing the longest average response distances and regular vehicles the shortest, as found in other studies (Gonzalez *et al.*, 2006, Fraser *et al.*, 1985; Grubb and King, 1991, Grubb *et al.*, 1992, Flemming *et al.*, 1988). However, similarly to Erwin (1989) in a study of waterbirds, response distances did not significantly vary with stage of breeding. Frequency of route use and mean season disturbance rate at a site was not related to response distance in contrast to my findings concerning the probability of a response and several other studies that suggest habituation to disturbance occurs (Gonzalez *et al.*; Miller *et al.*, 2001; Ikuta and Blumstein 2003).

Yalden and Yalden (1990) reported that golden plovers returned to chicks 5 - 83 minutes after a disturbance had passed. Gonzalez *et al.* (2006) found that time to return to nests was longest during the chick stage and when eagles were disturbed by birdwatchers and hunters. The time taken for egg and chick stage stone curlews to return to sites after an active response ranged from 0.2 minutes to 17.4 minutes but this was not significantly related to any measured variables.

A theoretical framework which has been applied to disturbance studies is the risk-disturbance approach (Frid and Dill, 2002) which uses economic models of anti-predator behaviour to study the responses of single species to human disturbance (Frid and Dill, 2002, Beale and Monaghan,

2004). Within this framework, individuals may trade off the avoidance of disturbance by humans against activities that may increase fitness, such as foraging, mating and parental care (Frid and Dill, 2002). The stone curlew is likely to make an assessment of the relative risk (to itself or to its nest or chicks) of fleeing or remaining in the area based on qualities attached to the PDA event. For example, at certain stages of the breeding cycle they may be more vulnerable, such as the egg or chick stage so their response may be to flee at larger distances and avoid being sighted by the predator or drawing attention to the nest site. People, and in particular those with dogs, may elicit a greater response than vehicles because they are more similar to natural predators of the stone curlew (Burger, 1981; Yalden and Yalden, 1990; Lord *et al.*, 2001). Until recently humans themselves have been predators through egg collecting and they still shoot stone curlews on migration in southern Europe and Africa (Green, Hodson and Holness, 1997). A larger group size may be perceived as representing a greater risk (e.g. Beale and Monaghan, 2004) either because more potential predators have a greater chance of success, or because it causes a larger 'loom rate' and so appears more threatening (Frid and Dill, 2002). In the case of vehicles, group size was significant in the models of alert responses but not for active responses. It is possible that this is related to noise that a larger group of vehicles makes, so that the bird may become alert sooner, but does not consider the actual risk to be greater and so the size of group does not affect the probability of running or flying.

Traditionally, this type of disturbance study is used to manage activities around nest sites. Often average response distances are used to set buffer zones or set back distances within which activity is minimised or excluded (e.g Richardson and Miller, 1997, Ronconi and St. Clair, 2002). If mean active response distance was used to manage access around stone curlew sites, the radius of the buffer zone would be 185 m. The problem with using response distance as a measure of tolerance, however, is that this distance represents the point at which the cost of remaining exceeds the cost of fleeing. This distance has been shown to be elastic and dependent on many factors, including some not measured in this study such as availability of alternative habitat or individual variability (Gill *et al.* 2001). Furthermore, there is no consensus over what type of response should be used to set buffer zones. Fernandez-Juricic *et al.* (2001) suggest alert distance should be used rather than flight distance as flight distance may not be a good indicator of tolerance, since it may be effected by other factors (Gill *et al.*, 2001), and buffer zones based on this measure would not included a buffer in which birds adapt their response to disturbance.

Gonzalez *et al.* (2006) and others (e.g. Stalmaster and Newman, 1978, Grub and King, 1991) improve the method of setting buffer zones by taking their models of probability of a response and using the percentiles of the predicted probability of flight, rather than the mean, as the distance for buffer zone radii. For example, the greatest distance at which imperial eagles were observed to respond to PDAs was 1000 m. The distance beyond which 1% of responses occurred was 800m and 5% of responses occurred beyond 450m. For stone curlews, the equivalent distances for the 0%, 1% and 5% percentiles of the response distance distribution (ranking from the largest distances downwards) are 1395 m, 683 m and 462 m respectively. In other studies the 30th percentile has been used (Stalmaster and Newman, 1978). For stone curlews this would be 180 m. This again demonstrates that even with quantitative models, a subjective decision about the radius of the buffer zone must be made. A buffer zone of 1395 radius around every stone curlew plot in Wessex would result in very little area left for access or military training, a management solution that is unlikely to be accepted and also may be unnecessary. Furthermore, the probability of active responses varies with many other factors and decisions would need to be made about how to manage sites with respect to these factors. For example, Gonzalez *et al.* (2006) and Beale and Monaghan (2004) suggest that buffer zones should be increased where human activities involve large groups of people, or large groups should be made to use alternative parts of the site. In the case of the stone curlew, this would be extremely difficult to achieve and costly to manage.

Another limitation of the approach used in this chapter is that an important aspect of the disturbance risk framework (Frid and Dill, 2002) is that animals should be able to track changes in the level of threat posed to them as the event proceeds (Bouskila and Blumstein, 1992). This method of analysing disturbance data does not allow this to be taken into account as there is no measure of the direction of travel, angles of approach or speed, or how distance changes over time.

Gill *et al.* (2001) and others have also criticised studies of this sort as they suggest that changes in birds' behaviour like those demonstrated in the studies described, may not necessarily mean that the birds suffer as a result of the disturbance. They suggest that the effect of a response is short-term and birds may be able to compensate for any effects of human disturbance. Therefore these types of studies may record the immediate effect of disturbance but they do not measure the impact on habitat use, survival, reproductive success or population size. Furthermore, they do not allow for the true discussion of behaviour in the context of predator risk as the ability to track

changes in the risk are not accounted for. However, in the absence of other improved data or techniques, behavioural studies of this sort remain a first measure of sensitivity and it may even be possible for the management of access based on a predicted probability of a response to a PDA event and measured response distances. In Chapter 4 and 5 I introduce a new method of measuring the behavioural response of stone curlews to disturbance that allows for greater application of the disturbance-risk framework.

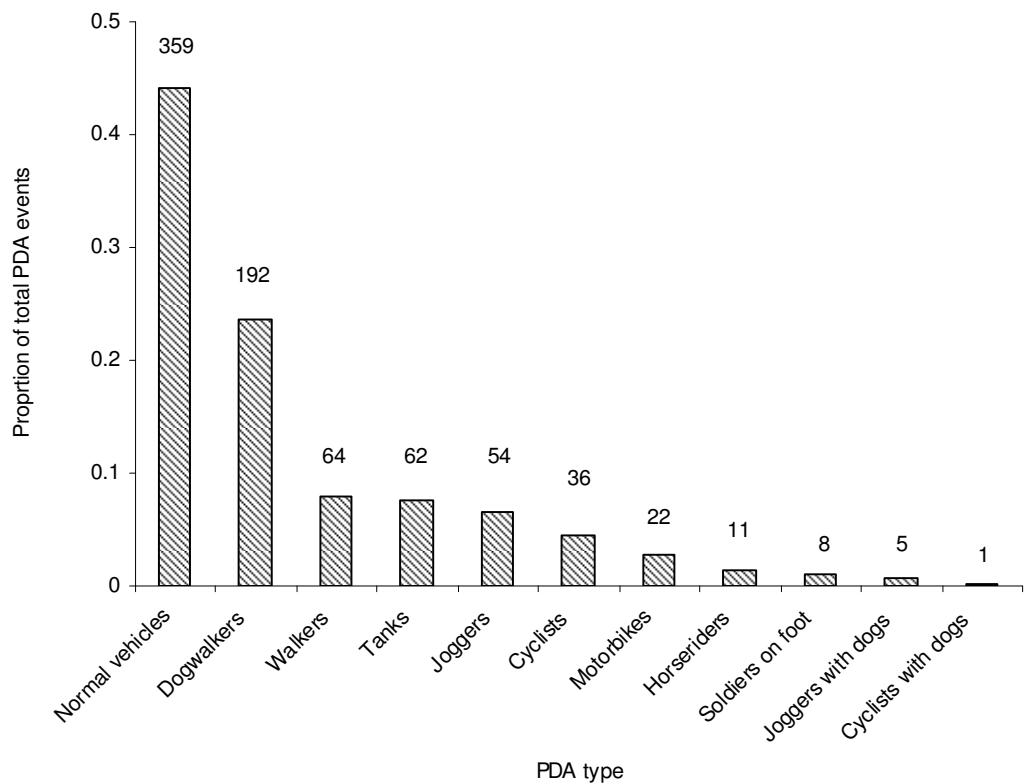


Figure 3.1. Proportions of PDA events at sites with stone curlews (N=814 encounters), excluding experimental disturbances. Bars show the proportion of the total PDA events that are represented by the PDA type. The actual numbers are shown above the bars.

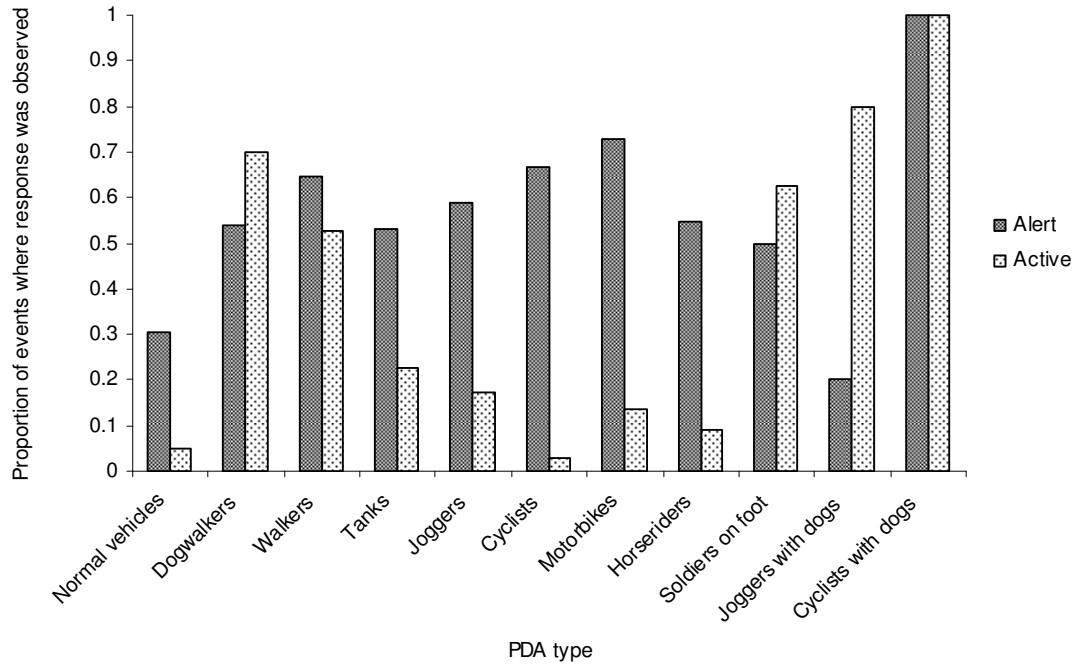


Figure 3.2. The proportion of PDA events (including experimental disturbances) of different types to which stone curlews responded by becoming alert or active.

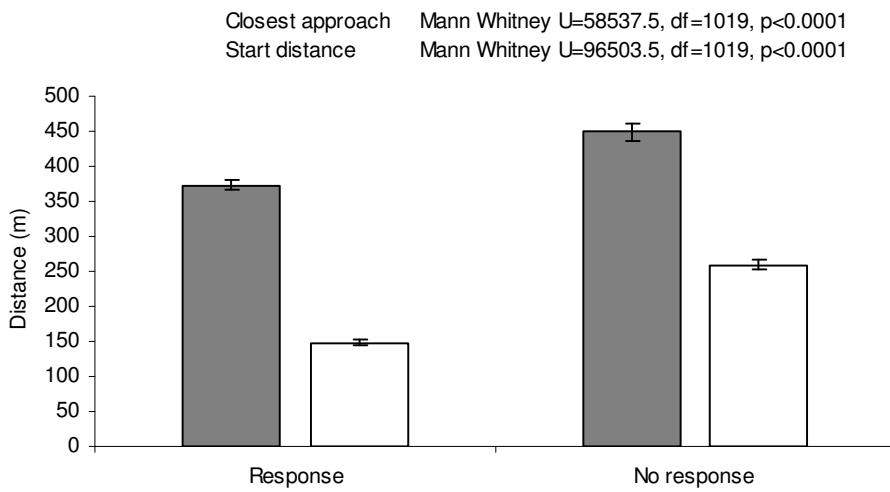


Figure 3.3. Comparison of the distance at closest approach and start distance between PDA events that caused a response of any kind and those that did not. Grey bars = start distance, white bars = closest approach. Means are shown +/-1SE.

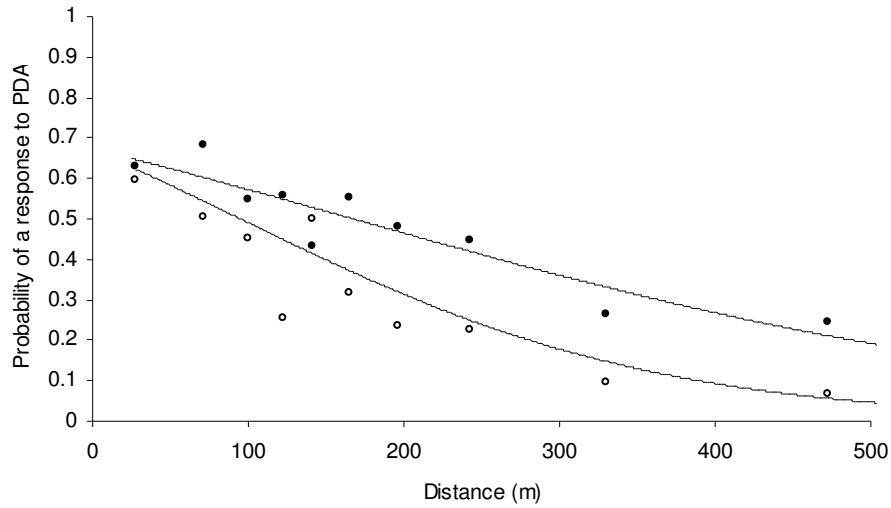


Figure 3.4. Probability per PDA events of an alert response (– ●) and active response (– - ○) by a stone curlew to all types of PDA event in relation to closest approach distance. The points are for the proportion of responses in distance bins and lines are fitted logistic regression models where only the distance variable is considered.

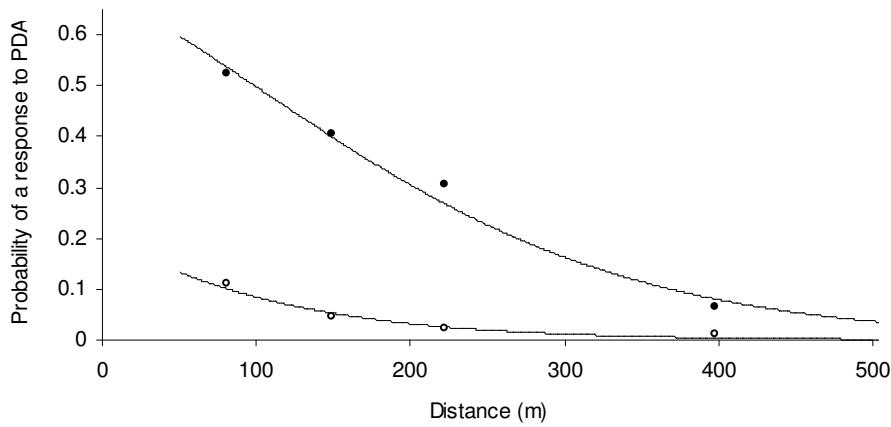


Figure 3.5. Probability per PDA event of an alert response (– ●) and active response (– - ○) by a stone curlew to vehicle PDA events in relation to closest approach distance. The points are for the proportion of responses in distance bins and lines are fitted logistic regression models where only the distance variable is considered.

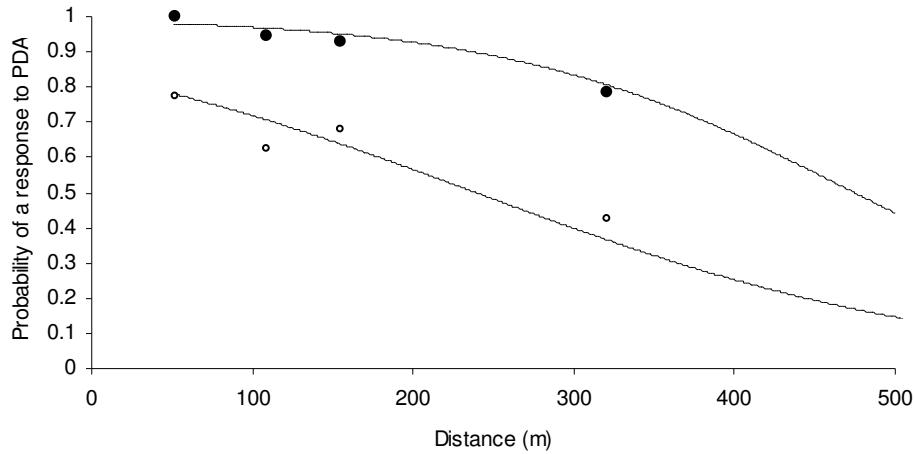


Figure 3.6. Probability per PDA event of an alert (– ●) active (– - ○) response by a stone curlew to people walking on foot PDA events in relation to closest approach distance. The points are for the proportion of responses in distance bins and lines are fitted logistic regression models where only distance is considered.

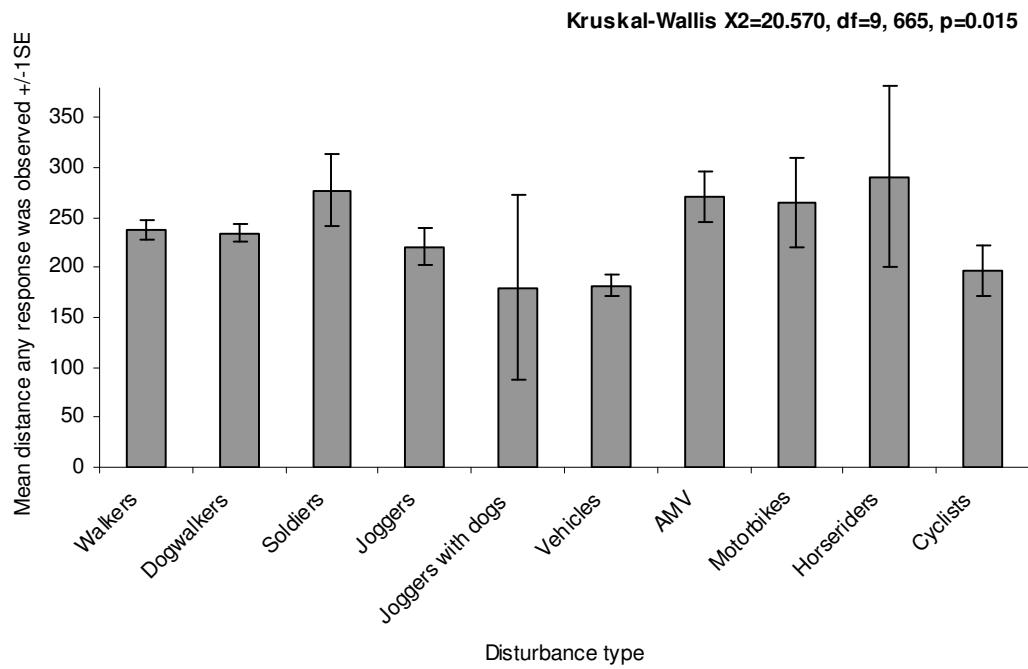


Figure 3.7. Differences in mean response distance between PDA types for any kind of response. Bars show mean response distance for each PDA type +/- 1SE.

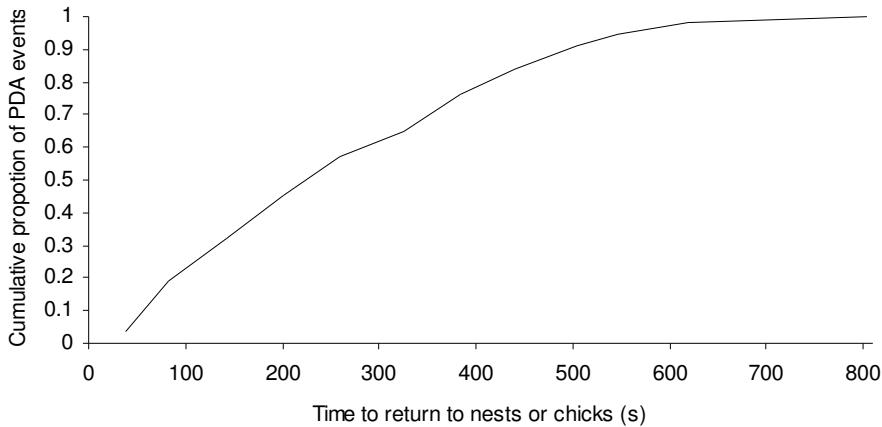


Figure 3.8. Cumulative distribution of time taken for stone curlews to return to nests and chicks after an active response.

Table 3.1. Candidate variables in logistic regression models to describe the probability of a response to a given PDA event

Variable	Description
Year	Factor with two levels: 2004 and 2005
Julian date	Continuous variable: days since 1 st January each year.
Frequency of use of route	Factor with two levels: frequently used route and infrequently used route
Stage of breeding	Factor with five levels: settlement, egg, chick, post-failure, roost
PDA type	Factor with varying number of levels: Full model = seven levels: person walking on foot, jogger, regular vehicle, tank, motorbike, cyclist, horse rider. Vehicle model = three levels: regular vehicle, tank, motorbike. Not included in people walking on foot model
Presence of dog	Factor with two levels: dog or no dog. Included in full models and people walking on foot models
Total agents	Number of components to PDA event e.g. number of people, number of vehicles, number of cyclists. Dogs were not included.
Closest approach on route	Continuous variable: closest approach the PDA makes to stone curlew throughout the duration of the event. Measured in metres.
Start distance	Continuous variable: the distance between the PDA and the stone curlew when the PDA first becomes visible to the stone curlew. Measured in metres.

Table 3.2. Numbers of responses of different types observed and the percentages of PDA events on which each toe of response occurred a) first responses and b) all responses, which include any subsequent responses after the first response.

a)

First response	Number of observations	Percentage of PDA events (N=1020)
Alert	494	48.5
Run	145	14.2
Fly	27	2.7
Active (run + fly responses)	172	16.9
Total	666	65.4

b)

Response	Number of observations	Percentage of PDA events (N=1020)
Alert	494	48.5
Run	291	28.5
Fly	57	5.6
Active (run + fly responses)	348	34.1

Table 3.3. Results of non-parametric tests examining whether there are differences in potential explanatory variables between PDA events where a response is observed or not observed. Means are shown for continuous variables and significant variables are highlighted in bold.

Variable	Response	No response	Test
Closest approach on route (m)	147.1	254.3	Mann Whitney U=61103.0, df=1019, p<0.0001
Start distance (m)	373.5	449.0	Mann Whitney U=96503.5, df=1019, p<0.0001
Julian date	148.6	151.3	Mann Whitney U=116224.0, df=1019, p=0.711
Season disturbance event rate	1.1	1.2	Mann Whitney U=104103.0, df=982, p=0.205
Year			$\chi^2=2.07$, df=1, p=0.1502
Route			$\chi^2=49.82$, df=1, p<0.00001
Stage of breeding			Kruskall-Wallis $\chi^2=21.63$, df=5, p=0.0006
Disturbance type			Kruskall-Wallis $\chi^2=313.49$, df=11, p<0.0001

Table 3.4. Parameter estimates from a logistic regression model relating the probability of an **alert** response of a stone curlew to all types of PDA event to explanatory variables. Coefficients for multi-level categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is people walking on foot for disturbance type).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, to the MAM. The residual deviance of the model 1230.92 with 1009 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	0.6710			
Year	0.8138	29.45	1	<0.00001
Disturbance type		69.82	6	<0.00001
Person walking on foot	0			
Jogger	-0.2076			
Normal vehicle	-1.3562			
Tank	-0.7317			
Motorbike	0.4814			
Cyclist	-0.2916			
Horserider	0.2209			
Total agents	0.2611	16.06	1	0.000061
Presence of a dog	-0.4767	5.90	1	0.015
Closest approach	-0.003717	44.82	1	<0.00001
Start distance		1.63	1	0.20
Stage		5.62	4	0.22
Julian date		0.080	1	0.77
Frequently used route		3.29	1	0.069

Table 3.5. Parameter estimates from a logistic regression model relating the probability of an **active** response of a stone curlew to all types of PDA event to explanatory variables. Coefficients for multi-level categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is people walking on foot for disturbance type).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, to the MAM. The residual deviance of the model 773.15 with 1006 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	1.8977			
Stage		12.27	4	0.015
Settlement	0			
Egg	0.08667			
Chick	0.4771			
Post failure	-0.7523			
Roost	-0.8322			
Disturbance type		130.22	6	<0.00001
Person walking on foot	0			
Jogger	-1.5805			
Normal vehicle	-2.7524			
Tank	-1.2101			
Motorbike	-1.7537			
Cyclist	-2.3532			
Horserider	-2.8984			
Frequently used route	-0.9729	18.23	1	0.000019
Presence of a dog	1.2288	32.30	1	<0.00001
Closest approach	-0.007928	93.86	1	<0.00001
Start distance		0.55	1	0.45
Year		3.78	1	0.051
Julian date		1.15	1	0.28
Total agents		0.69	1	0.40

Table 3.6. Parameter estimates from a logistic regression model relating the probability of an **alert** response of a stone curlew to vehicle PDA event to explanatory variables. Coefficients for multi-level categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is normal vehicles for disturbance type).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, to the MAM. The residual deviance of the model 447.45 with 438 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	0.1928			
Disturbance type		15.73	2	0.00038
Normal vehicles	0			
Tank	0.5553			
Motorbike	1.89397			
Total agents	0.3352	19.14	1	0.000012
Closest approach	-0.0077	55.22	1	<0.00001
Stage		6.55	4	0.16
Start distance		2.99	1	0.083
Year		0.012	1	0.91
Julian date		1.089	1	0.29
Frequently used route		3.09	1	0.078

Table 3.7. Parameter estimates from a logistic regression model relating the probability of an **active** response of a stone curlew to vehicle PDA event to explanatory variables.

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, to the MAM. The residual deviance of the model 165.77 with 440 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	1.0684			
Frequently used route	-2.8504	47.76	1	<0.00001
Closest approach	-0.0009615	14.34	1	0.00015
Disturbance type		5.34	2	0.068
Total agents		0.21	1	0.64
Stage		0.91	4	0.92
Year		0.59	1	0.44
Julian date		1.61	1	0.20
Start distance		1.19	1	0.27

Table 3.8. Parameter estimates from a logistic regression model relating the probability of an **alert** response of a stone curlew to people walking on foot PDA event to explanatory variables.

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, to the MAM. The residual deviance of the model 558.17 with 444 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	0.004022			
Year	1.4137	39.03	1	<0.00001
Presence of dog	-0.4973	5.88	1	0.015
Closest approach	-0.002778	8.88	1	0.0028
Start distance	0.006161	8.58	1	0.0033
Frequently used route		0.0020	1	0.96
Stage		2.21	4	0.69
Total agents		0.24	1	0.62
Julian date		0.18	1	0.66

Table 3.9. Parameter estimates from a logistic regression model relating the probability of an **active** response of a stone curlew to people walking on foot PDA event to explanatory variables. Coefficients for multi-level categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is settlement for stage).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, to the MAM. The residual deviance of the model 485.34 with 440 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	1.6367			
Frequently used route	-0.6128	4.82	1	0.028
Stage		18.84	4	0.00084
Settlement	0			
Egg	0.4193			
Chick	0.7847			
Post failure	-1.0424			
Roost	-0.9111			
Presence of dog	1.1907	27.80	1	<0.00001
Year	-0.6383	7.028	1	0.00080
Closest approach	-0.0081	68.38	1	<0.00001
Total agents		3.69	1	0.054
Start distance		1.59	1	0.20
Julian date		0.98	1	0.32

Table 3.10. Response distances for responses of different kinds

Descriptive of response distance	Any	Alert	Run	Fly	Active
Mean	229.20	241.58	192.68	131.89	184.76
Median	192.00	216.00	163.00	113.00	161.00
SD	134.20	137.81	106.83	87.07	106.70
Minimum	20.00	22.00	10.00	10.00	10.00
Maximum	738.00	738.00	659.00	420.00	659.00

Table 3.11. Pearson correlations between response distance, closest approach and start distance.

	Closest approach	Start distance
Response distance	r 0.704	0.603
	n 666	666
	p <0.0001	<0.0001
Closest approach	r	0.390
	n	666
	p	<0.0001

4 Predicting the probability of a behavioural response by stone curlews to disturbance by humans

4.1 Summary

Statistical models are produced that describe the probability of a stone curlew showing an alert or active response, per unit distance traversed by a potential disturbance agent (PDA). The probability of response was influenced by the distance between them and the PDA, PDA type, speed, stage of breeding and regularity of use of the route taken by the PDA. These effects are discussed in the context of the evolution of stone curlew anti-predator responses. There was also a suggestion that older birds and those with more breeding experience tolerate disturbance to a greater extent than young bird and first-time breeders.

4.2 Introduction

Chapter 3 described response distances and probabilities of responding based upon observations of stone curlew behaviour during PDA events. However, in common with most behavioural studies (e.g. Burger 1981, 1991, 1994; Yalden and Yalden, 1990; Yalden 1992; Fitzpatrick and Bouchez 1998; Lafferty, 2001), these analyses consider a *response per event*, and so are restricted in their usefulness. For example, management decisions based on response distances alone could mean impractically large buffer zones. Buffer zones are often defined by extending the edge of the breeding or roosting sites by adding the alert distance or flight initiation distance (e.g. Gonzalez *et al.*, 2006, Fernandez-Juricic *et al.*, 2001). For stone curlews in a flat landscape, circular buffer zones around a nest sites with a radius of the alert and active response distances (241.58m and 184.76m) from Chapter 3 would be 0.18 km² and 0.11 km² respectively.

However, potential disturbance events are often of long duration and the potential disturbance agent (PDA) varies in its location and movement relative to the bird. Therefore, the probability of a response can vary throughout the event with factors associated with the disturbance. In this chapter I present a new method of assessing the behavioural response of stone curlews to human disturbance by considering the probability of a *response per unit distance travelled* by the disturbing event along its route of movement. This allows the consideration of many factors relating to the disturbance event that change over time during the event, and can help understand why particular responses are shown to disturbance. This approach also allows the discussion of human disturbance in the risk-disturbance framework of Frid and Dill (2002), which uses models

of predation risk to suggest how animals will respond to disturbance by humans. These authors suggest that the plasticity of flight initiation distance is based on the optimisation of tradeoffs and so is likely to vary with changes in the human-induced stimuli in the same way that it would vary with predation risk.

4.3 Aims of the chapter

The aims of this chapter are to:

- 1) Describe a new method of measuring stone curlew behavioural response to PDA events.
- 2) Present minimal adequate models to predict alert and active responses by stone curlews to all types of PDA event.
- 3) Present minimal adequate models to predict alert and active responses by stone curlews to *specific types* of PDA event.
- 4) Establish if there is any evidence of habituation to disturbance by older or more experienced stone curlews, or on sites with a higher disturbance event rate.

4.4 Methods

Sites were selected using the method described in section 2.4.1. Stone curlew and disturbance survey protocol followed the methods described in sections 2.4.2 and 2.4.3.

4.4.1 Measuring the behavioural response of stone curlews to PDAs

The method for measuring a behavioural response of stone curlews to PDA events followed the same methods described in section 3.4.1 and I considered the two behavioural responses *alert* and *active* as described in section 3.4.3.

4.5 Data preparation and analysis

The probability of a behavioural response by the stone curlew can be modelled as a function of the variables measured during each PDA event (Table 2.1), by treating responding or not as a dependent binary response variable which is a function of independent or explanatory variables. In Chapter 3, the probability of a response was modelled as a binary response variable as a function of independent variables but the binary response was whether the stone curlew responded at any time for the PDA event. To give these analyses higher resolution, I used the mapped disturbance routes to treat each PDA event as a succession of binomial trials during which the bird under observation had the opportunity to respond or not. These trials are taken to be successive points 1 mm apart along the route traversed by the PDA.

I used the map of the PDA event and the viewshed to obtain the coordinates of start distance, changes in direction (waypoints), end point and the point at which a response was observed. A Visual Basic computer programme written by R.E Green was used to divide these routes into 1-millimetre sections (Figure 4.1). In each millimetre section traversed by a PDA along a route, a watched bird could either respond in a particular way or not (the binary response). The location of the PDA was interpolated at these millimetre intervals along the route using the start time, waypoint times and end times and from these locations the distance between the focal bird and the PDA and the speed and direction of movement of the PDA were calculated.

PDA velocity was resolved into two components using the computer programme:

- 1) **Speed to fro** – distance travelled per unit time (m/hr) in the direction towards or away from the bird. Movement towards the bird was treated as positive. Movement away was treated as negative.
- 2) **Speed side** – distance travelled per unit time (m/hr) along the line at right angles to the line joining the bird and PDA. This component was treated as positive regardless of direction.

The variables in Table 4.1 were used as independent variables in logistic regression models. Minimal Adequate Models (MAMs) were selected to predict the probability of occurrence of a response using logistic regression with a backwards-elimination model selection procedure (Crawley, 2002). A hypothetical example of a MAM which predicts the probability of a response to a PDA could be:

$$\text{logit}(k) = a + b_1 * (\text{bird to PDA distance}) + b_2 * (\text{stage of breeding}) + b_3 * (\text{PDA type})$$

Where k is the probability of a response and a and b are fitted constants from the logistic model. In this case, stage of breeding and PDA type are factors with several states, so the b values for these actually represent groups of coefficients for each factor.

Once a bird had responded, e.g. by becoming alert, it was then assumed not to be available to respond in the same way again, so all subsequent data for that PDA event was discarded from the alert analysis. Birds sometimes became alert before running or flying, so data after an alert

response could still be used for the analysis of active responses. Once a bird had run or flown it was considered not to be available to respond again in this way to that particular PDA event. Birds sometimes ran before flying, but there were insufficient data to warrant modelling running and flying as separate responses. Therefore, a running or flying response, whichever occurred first was taken as terminating the event. This modelling approach is similar to that used in survival analysis; for example by proportional hazards methods. Not having yet responded during the traverse of 1 mm section of route can be considered to be like surviving a time interval.

4.6 Results

I firstly present the results of using just the distance variables (the distance between the PDA and the stone curlew at each point along the route, and the distance the PDA just became visible to the stone curlew) to predict the probability of a response to any disturbance event before using all candidate variables (Table 4.1) to select the MAMs.

4.6.1 Probability of a response in relation to distances between the stone curlew and the PDA

As expected, stone curlews show an increased probability of alert and active responses occurring per unit distance traversed by the PDA when the distance between the bird and PDA decreases (Figure 4.2). However, even at large distances (in excess of 500m), stone curlews have an elevated probability per metre of responding to a PDA event by becoming alert or making an active response.

The probability of a reaction is also affected by the distance between the stone curlew and the PDA when it first becomes visible to the stone curlew. Stone curlews are more likely to respond if the PDA first becomes visible at closer distances (Figure 4.3).

4.6.2 Minimal adequate model of factors affecting the probability of an alert response to a PDA

When all PDA types are combined, the model to predict an alert response contains almost all the explanatory variables measured (Table 4.2). Controlling for distance from the PDA, stone curlews are more likely to become alert when at the egg or chick stage (Figure 4.4), if the disturbance is on an infrequently used route (Figure 4.5), if the disturbance is by people on foot rather than vehicles (Figure 4.6), and if PDA group size is large. There was also a significant difference between years in this model (Figure 4.7). Both components of speed were also

included in the MAM. Stone curlews were more likely to respond if the side to side speed was slow or if the to-fro speed was high and towards the bird. The probability of an alert response, however was not significantly affected by the presence or absence of a dog or start distance.

4.6.3 Minimal adequate model of factors affecting the probability of an active response to a PDA

The minimal adequate model for active responses included many of the explanatory variables (Table 4.3). The only differences in parameters between the alert and active models were that the presence of dogs was a significant factor and PDA group size was excluded.

Active responses were more likely in 2004 than 2005 (Figure 4.8), on an infrequently used route (Figure 4.9), in the presence of a dog (Figure 4.10) and people walking on foot (Figure 4.11). As with alert responses, active responses were more likely at the chick and egg stage (Figure 4.12).

Again, both components of speed are in the model. Stone curlews are more likely to respond actively to slower speeds in the sideways component but if the PDA is heading quickly straight towards the bird, the probability of an active response is higher.

The presence of almost all explanatory variables in the minimal adequate models, and the highly significant effect of *PDA type* in both models, suggests that more meaningful models can be created by splitting disturbance stimuli into groups of containing similar types of PDA. In the next set of analyses, models are presented for:

- 1) People walking on foot (recreational walkers and soldiers)
- 2) All vehicles (including military vehicles and motorbikes)
- 3) Other PDA types. This group comprises the data for joggers, horse riders and cyclists.
The data set was small for each of these PDA types, so they were not modelled separately.
- 4) Non vehicle PDA types. The group comprises data for walkers, soldiers, joggers, cyclist and horseriders.

Alert and active response models are presented for each of the four groups.

4.6.4 Minimal adequate model of factors affecting the probability of an alert response to people on foot

As expected the most significant variable in this MAM was distance between the stone curlew and the person (Table 4.4). There was also a significant difference between years with alert responses being more likely in 2005 than 2004 (Figure 4.13), and the route was infrequently used (Figure 4.14).

4.6.5 Minimal adequate model of factors affecting the probability of an alert response to vehicles

The minimal adequate model for alert responses to vehicles included most of the candidate explanatory variables (Table 4.5). The only non-significant terms were year, Julian date and stage in the breeding cycle. Stone curlews were more likely to respond to vehicles on infrequently used routes (Figure 4.15), and to larger groups of vehicles. There was a significant difference in the probability of response for different vehicle types (Figure 4.16), with motorbikes and tanks having a higher probability of response than other vehicles. The probability of response declined with increasing distance between the PDA and the bird and also with increasing distance at the start of the event.

4.6.6 Minimal adequate model of factors affecting the probability of an alert response to other types of PDA

The probability of an alert response to joggers, horse riders and cyclists (Table 4.6) is elevated with decreasing distance between the PDA and the stone curlew, increasing rate at which the PDA is approaching the bird, decreasing Julian date and if the PDA is on an infrequently used route (Figure 4.17).

4.6.7 Minimal adequate model of factors affecting the probability of an alert response to non vehicle types of PDA

In this MAM, the different types of PDA produced significantly different probabilities of response (Table 4.7). People walking on foot produced higher response probabilities than joggers, cyclists or horse riders (Figure 4.18). The probability of response was higher in 2004 than 2005 and decreased as the date increased. The chick and egg stage also produced higher response probabilities (Figure 4.19), as did PDAs on infrequently used routes (Figure 4.20).

4.6.8 Minimal adequate model of factors affecting the probability of an active response to people on foot

The probability of an active response to people on foot (Table 4.8) was elevated if there was a dog present (Figure 4.21), varied with stage of the breeding cycle (Figure 4.22) and was higher if the person was moving rapidly towards the stone curlew (Figure 4.23).

4.6.9 Minimal adequate model of factors affecting the probability of an active response to vehicles

In addition to distance, the MAM of active responses to vehicles (Table 4.9) included the route the vehicle was taking was frequently used or not. Vehicles on a route less frequently used were significantly more likely to produce an active response those on well known routes (Figure 4.24). In addition, the probability of an active response was negatively related to the sideways component of speed, so slower vehicles were more likely to evoke an active response.

4.6.10 Minimal adequate model of factors affecting the probability of an active response to other types of PDA

In this MAM, the different types of PDA produced significantly different probabilities of response (Table 4.10). Joggers produced higher response probabilities than cyclists or horse riders.

4.6.11 Minimal adequate model of factors affecting the probability of an active response to non vehicle types of PDA

The MAM to describe an active response to non vehicle PDA events comprised the stage of breeding (Figure 4.25), PDA type, speed to fro, presence of a dog (Figure 4.26) and distance between the stone curlew and the PDA (Table 4.11).

4.7 Bootstrapping of models to avoid pseudoreplication

At first sight it might seem that my logistic regression analyses are pseudoreplicated in two ways. First, each PDA event is represented by many thousands of short route sections. However, this does not represent pseudoreplication because a response can occur only once (if at all) within one PDA event. Changing the size of the route sections therefore does not change the outcome of tests of statistical significance. Second, I collected information on multiple PDA events from the same breeding site. These observations are pseudoreplicated because the different PDA events at the same site are not truly independent. Outcomes for the same site might be similar to each other

because of unmeasured variables common to all PDA observations at that site. To avoid the effects of this on significance tests, an R programme was written by A. Manica and R. E. Green to carry out bootstrap significance tests. For each of 1000 bootstrap replicates, I drew a sample of data consisting of all the data for each of n sites selected at random with replacement from the n sites for which data were available. Hence, data for a particular site could be present in the bootstrap sample several times or not at all. The model was fitted to each bootstrap sample of data and the significance of each effects was tested using Helmert contrasts (Crawley, 2002). Stepwise model selection by backwards elimination then proceeded as before. The p values from the bootstrap estimates for the motor vehicle and non motor vehicle models are shown in Tables 4.7 and 4.11. Backwards stepwise model selection selected the same variables in the finals MAMs.

4.8 Summary of models

A summary of the significant variables in the models and the direction of relationships are presented in Table 4.12.

4.9 Effects of habituation on probability of response to disturbance

I considered two variables that might indicate whether stone curlews were becoming habituated to disturbance. These were:

- 1) Age of the focal bird, determined from colour rings.

All birds were adults (1 year old or more). I assumed that, if habituation occurs, an older bird would have experienced more potential disturbance than a young one and would be less likely to respond.

- 2) The average season disturbance event rate at the site.

I assumed that, if habituation occurs, the probability of response to a given event would be lower at a site where events occur more frequently.

Age and average disturbance data were not available for all events or sites so I did not include these variables among the candidates in the analyses described above. Instead, I took each MAM selected in the procedure described above, fitted it to the reduced set of data for a habituation variable and then added that habituation variable to the model and assessed its effect by a likelihood-ratio test. I only carried out such an analysis if there were at least 20 responses available.

4.9.1 Age of stone curlew

Young adult stone curlews were more likely than older birds to respond to vehicles and non vehicle PDA events by becoming alert. Younger birds were also more likely to respond to people walking on foot and non motor vehicle PDAs by making an active response (Table 4.13). Age was represented in this case as a continuous variable. The effect of experience can also be tested by treating one and two year old stone curlews as probable first time breeders with little experience of disturbance, and the remainder as more experienced birds (2 level factor). In this case too, probable first time breeders were more likely to become alert to vehicle PDA events, and make an active response to non vehicle PDAs (Table 4.14).

4.9.2 Average frequency of PDA events per hour at the site

Using the season disturbance event rate, there was no significant effect of average disturbance event rate at a site on the probability of a response to PDA events (Table 4.15).

4.10 Discussion

Inspection of the graphs presented here, and examination of the fitted models, shows that the probabilities of alert and active responses (running and flying) were low when PDAs were very distant, but showed signs of increasing from these low levels even when the distance between the PDA and the bird was large. In many cases there was evidence of an increase in active response probability when the PDA was 300-400 m away. It therefore appears that stone curlews may be more sensitive to disturbance than some other wader species and may be more similar to raptors in their responses (as discussed with reference to response distance and probability of responding to PDA events in Chapter 3). For Spanish imperial eagles *Aquila adalberti* the probability of a response increased sharply when activities occurred at less than 450 m from the nest, but was negligible if they occurred at 800 m (Gonzalez *et al.*, 2006). These distances are similar to those recorded in other large raptors such as golden eagle *Aquila chrysaetos* (Holmes *et al.*, 1993), and slightly higher than those recorded in bald eagle *Haliaetus leucocephalus* (Stalmaster and Newman, 1978; Fraser *et al.*, 1985; Grubb and King, 1991).

In addition to distance between the PDA and stone curlew, other variables were found to influence response probability. Before splitting PDA types into similar groups, the MAMs for alert and active responses comprised almost all explanatory variables. However, I consider that these models run a risk of being unrealistic because they combine such different PDA types as

dogwalkers and tanks. By splitting the PDAs into groups of similar types, simpler MAMs were produced and it is hoped that the models are therefore more realistic.

Stone curlews may become alert to a PDA without showing any noticeable response (Arroyo and Razin, 2006), making the identification of such a response difficult. In addition, it also seems likely that alert responses are of less biological significance than active responses (see Chapter 3). For these reasons, the majority of the discussion will place emphasis on the active response as this was measured more clearly and probably has the greatest impacts.

Although fitness is associated with many factors, for many species one of the most important variables affecting fitness is probably nest predation (Ricklefs, 1969). As a result, animals have evolved a variety of adaptations, such as crypticity, nest defence behaviour and specific responses to predators to reduce the fitness consequences of predation. There are two main hypotheses concerning how animals respond to predators and at what distances an animal will flee. The first is termed the “perceptual limit hypothesis” and states that flight distance from an approaching predator is constrained only by an animal’s ability to detect it, and assumes that the prey will flee as soon as the predator is detected. If predators are difficult to detect until they are close, it is more likely that animals will respond as soon as the predator is visible and that this distance will be the only determining factor of the response. For example, when visibility is severely restricted due to dense vegetation or the landscape topography, a predator may only be detected once it is inside the distance at which the prey would have otherwise fled. In this situation, there are no tradeoffs or decisions being made by the prey about how to respond, and the flee response is shown as soon as the risk is detected (Ellis, 1982). This is often termed an “ambush” response (Ydenberg and Dill, 1986).

Ydenberg and Dill (1986) suggest a second hypothesis which they term the “economic hypothesis” because it considers decisions animals make when faced with a predator. The prey can be thought of as having to continually choose between remaining at a site or fleeing as a predator approaches. The underlying theory of the economic model is that responding to a predator may have costs as well as benefits, and so flight distance will vary accordingly. The model predicts that the optimal response distance is the point at which the cost of remaining exceeds the cost fleeing and that flight distance should increase with increasing cost of remaining and decrease with increasing cost of flight.

Many authors have likened the way in which animals respond to disturbance with the way they respond to predators (Walther, 1969, Frid and Dill, 2002). The idea that animals view human disturbance in a similar way to predation risk was first suggested by Walther (1969). In an experiment with a vehicle, Walther approached Thompson's gazelles *Gazella thomsoni* and measured flight initiation distance. This was compared to the animal's natural response to wild dogs *Lycaon pictus* and other predators, and as the response was similar, it was assumed by Walther that disturbance from humans or vehicles was viewed similarly to predators and the predation risk. Since Walther's work the extrapolation of the predator framework to disturbance studies has been widely discussed (e.g. Berger *et al.*, 1983, Madsen, 1994, Gill *et al.*, 1996, 2001, Gill and Sutherland, 2000), and is referred to as the risk-disturbance hypothesis by Frid and Dill (2002). Like the economic model, the risk-disturbance hypothesis predicts that responses by disturbed animals are determined by changes in factors associated with the disturbance stimuli. Stronger reactions should be observed when the risk is higher. Risk is assessed by the animal and is likely to depend upon a complex mix of variables.

The comparison between predation risk and disturbance is intuitive because the effort in responding to both predators and human disturbance diverts time from other activities and cost-benefit trade-offs may be similar. However, there are two criticisms. Firstly, most disturbance stimuli are too recent for animal responses to reflect adaptation, whereas animals have evolved specific anti-predator responses (e.g. Walther , 1969, Ghalambor and Martin, 2000). However, Dill (1974 a,b) show that prey respond to a stimulus when it exceeds a tolerance threshold, even when the 'predator' is new to the prey's evolutionary history (see comments on loom rate below). The second criticism is that disturbance stimuli do not carry the same risk as predators because there is not the obvious risk of death from disturbance stimuli that there is from a predator. However, Frid and Dill (2002) suggest that predation *risk* differs from predation itself and an animal's response to a predator is based on a calculation of this risk and a compromise between its activity (e.g. incubation eggs or feeding in a particular area) and the risk of predation. Calculation of predation risk is based on factors such as the structure of the environment and the behaviour of the predator, and anti-predator behaviour responds to changes in *these* factors rather than the predation *rate*, it therefore seems likely that responses to non-lethal disturbance events will follow the same decision making processes.

By considering human disturbance in a predator risk framework, where the ‘prey’ view a PDA event as a ‘predator’ we can begin to understand the reasons for responses. Prey will allow a predator to approach up to a certain point before initiating escape behaviour (Ydenberg and Dill, 1986, Lima and Dill, 1990). This suggests that response distances are not fixed within a species, but may increase in riskier situations as an outcome of a cost-benefit assessment by the prey. This is referred to as the plasticity of flight (Frid and Dill, 2002), and is based on the optimisation of trade-offs (Lima, 1998, Lima and Dill, 1990). In the framework of this model, the distance a stone curlew will respond to disturbance will be determined by a balance between the costs of fleeing and remaining. As the costs of remaining increase (increased risk), flight distance increases, and therefore the response is a function of distance between the PDA and the stone curlew but also other factors associated with the risk.

Pre-breeding, post failure, at post breeding roosts and on wintering grounds, the *cost* to the stone curlew may be predation. However, responses to predators and disturbance are more complicated when stone curlews are breeding. In this study the response probability was greatest at the egg and chick stage. At these stages of the breeding season the stone curlew has made a large reproductive investment and must trade-off the costs and benefits of responding depending on the risk to itself as well as the risks to the nest or chicks. Leaving nests when potential predators approach may be a strategy to reduce the vulnerability of eggs or chicks to potential predators (Montgomerie and Weatherhead, 1988). Whilst incubating or brooding chicks, the cryptic markings of the stone curlew makes it hard for potential predators to locate them. However, by moving away in response to predators, the stone curlew runs the risk of attracting the attention of the predator and leading them to the nest site or chicks. This is the trade off. At longer distances, the stone curlew may draw attention to *its* location but either the predator will not notice in time or it will not be able to get a good fix on the site where eggs and chicks were left. However, at shorter distances, predators are more likely to locate the stone curlew themselves and obtain a good fix on the nest or chicks. Therefore it is beneficial for the stone curlew to discern the threat posed by the predator by collecting as much information as possible about the threat in order to assess the trade-off and respond appropriately.

Many of the trade-offs associated with responding to disturbance during breeding can be compared with the decisions made by birds when determining how to show nest defence behaviour to potential predators (see review by Montgomerie and Weatherhead, 1988). Stone curlews do not exhibit nest defence behaviour such as injury feigning, pseudo-sleeping or false

incubation although they sometimes alarm call when disturbed (E. C. Taylor, pers. obs). However, there are several aspects to do with parental characteristics which have been shown to effect intensity of nest defence that may also be associated with a bird's response to predation or disturbance. For example, Barash (1975) suggested that a bird's re-nesting potential should have an important effect on its willingness to take risks in defending its nest. The maximum response should be where the potential for re-nesting in that breeding season is zero (Barash, 1975). This is because the value of a brood is directly proportional to the cost of replacing it (Dawkins and Carlisle, 1976, Boucher, 1977). Therefore by transferring this hypothesis to responses to disturbance, if the main risk is to the eggs or chicks, parents should alter their response with respect to the investment in the eggs and chicks and the cost of replacing them. As a result, there may be a more severe response later in the incubation period or when chicks are near fledging. In a precocial species such as the stone curlew, responses may be greatest at hatching before chicks leave the nest. In this study the response was greatest at the chick stage. Chicks are easier for predators to see than eggs as they are mobile and larger and so by moving away from young early, predators may be distracted by the parent and unable to locate the chicks.

Response probability was lowest during the roost stage. It may be thought that autumn roosts are a high risk time in the breeding cycle because flight ability is impaired by moulting of flight feathers. However, at this time stone curlews gather together (with in excess of 50 individuals observed) and perceived risk may be lowered as a result of corporate vigilance (Pulliam, 1973) or the dilution of risk and 'safety in numbers' (Kenward, 1978).

In order to assess the risk and respond appropriately, animals need to gather as much information as possible about the predator or disturbance. The explanatory variables in the MAMs presented in this chapter can assist in the evaluation of risk by stone curlews. Frid and Dill's (2002) risk-disturbance hypothesis model seems to suggest that animals make decisions in a complex cognitive way, however, this may not be true. Ydenberg (1984) suggest that animals may use simple 'rules of thumb' to decide when to respond. This idea was expanded by Bouskila and Blumstein (1992), who suggest that animals do not need perfect information in order to respond accurately. The zone of tolerance is generally shifted to over estimate the risk and animals should attempt to track changes in the risk through time rather than act on the average risk hazard of the event.

Ydenberg and Dill (1986) suggest that, as not all animals detected by prey will be dangerous, and not all predators will represent equal risk, it is advantageous to the prey to be able to distinguish between them so that the response is based on calculation of the actual risk. The ability to make distinctions between predators has been observed in many species, for example, reef fish (Potts, 1981), and redshanks *Tringa totanus* (Cresswell, 1993). In the disturbance literature, differential responses to PDA types are widely reported (Gonzalez *et al.*, 2006, Richardson and Miller, 1997). Stone curlews can clearly distinguish between PDA types as their response to the different PDA groupings was significantly different. In particular, there was a higher probability of an active response per unit distance traversed by the PDA when the disturbance event involved people on foot and non motor vehicles compared with motor vehicles. People are predators of stone curlews, historically through egg collecting, and currently through hunting whilst on migration (Green *et al.*, 1997). Furthermore, and in common with other studies, the presence of a dog with a walker led to a higher probability of response by a stone curlew than a walker alone (Burger, 1981; Yalden and Yalden, 1990; Lord *et al.*, 2001). Given that dogs most closely resemble an actual predator of stone curlews, this result is not surprising. There is a direct threat to the parents as dogs have been observed catching and killing waders (Burger, 1981), and it is also more likely that dogs can locate cryptic nests and eggs than a person (Lord *et al.*, 2001). By flushing at greater distances where dogs are present, removing themselves from the nest site and staying away until the danger passes, stone curlews reduce the chance that their own movement and location will reveal the location of the nest or chicks. The majority of dogs in this study were off a lead but walking alongside the walker. Unfortunately, there were insufficient data to test for a difference between dogs on and off leads. This is an important aspect to address (possibly through more experiments) for the management of access as there is thought that birds can identify a leashed and unleashed dog and adapt their response accordingly (Lord *et al.*, 2001).

Some studies have measured the actual speed at which the PDA is approaching and tested its significance in determining a response (Lord *et al.*, 2001, Wilson *et al.*, 1991). A study of breeding New Zealand dotterels *Charadrius obscurus* showed no effect of speed on measured responses, whilst studies on Adelie penguins *Pygoscelis adeliae* and reindeer *Rangifer tarandus platyrhynchus* suggest speed of approach is important, with faster approaches evoking greater responses than slower ones. We split speed into its two components described in section 4.5 - *speed to fro* and *speed side to side* because there is evidence that animals can distinguish between a direct and tangential approach by predators and may make assessments of the risk based on this information. The inclusion of speed to fro in many of the MAMs presented is interesting and

indicates that stone curlews may be able to distinguish PDA events that are approaching quickly and directly, from those that are approaching slower or moving away. This aspect of response is widely supported in the literature for a range of taxa (Burger and Gochfield, 1981, 1990, Cooper, 1997, 1998). For example, in a controlled experiment where people on foot approached adult keeled earless lizards *Holbrookia propinqua* (Cooper, 1998), from set distances lizards were more likely to flee where the person turned directly towards them. It was not possible in this case to determine whether the escape decision was based on the new orientation in relation to the lizard's distance from it, or on the abruptness of the change in direction, or a combination of the two. However, it was considered that the cue to respond was facial view and eye contact, as these aspects of predators are important indicators of threat in lizards (Burger *et al.*, 1991, Burger and Gochfield, 1993).

As stone curlews react at long distances, it is unlikely that facial view and eye contact is the mechanism behind their response to direct and tangential approaches. An alternative cue is loom rate as suggested by Frid and Dill (2002). Under this premise, stone curlews respond with increasing probability as the object gets bigger and perceivably more threatening. 'Loom rate', the speed and size of an approaching risk has had limited discussion in disturbance literature, although is prominent in predator response work. Dill (1974a and b) exposed zebra danio fish *Brachydanio rerio* to real predators, a model of a predator and a film of a black dot which increased in size and simulated an approaching predator. In all three cases, the threshold depended on the size and speed of the approaching predator, with responses similar across all predator types. This indicated that danios decided to flee when the loom rate exceeded a margin of safety regardless of whether the predator was real.

It is interesting that the most important components of speed that affect active stone curlew responses differ between the people walking on foot and vehicles. As already discussed, stone curlews show an increased response to people walking on foot when they are heading quickly, directly towards them. This variable was not significant in the vehicle active model, but the sideways component of speed was significant. Risk is thought to be elevated with increased speed because the threshold loom rate is exceeded faster (e.g. Walther, 1969, Kitchen, 1974, Dill, 1974a, Webb, 1981). However, vehicles with *slow* side to side speed were more likely to initiate an active response. This negative relationship between speed and probability of a response is unusual but supported by a small number of studies (e.g. Hurley and Hartline, 1974, Hutson, 1982). The effect may be due to slow vehicles being present for longer periods, and this being

associated with a higher risk of detection or capture. Additionally, whilst vehicle type was not significant in the model, slower vehicles are more likely to be tanks, which through their size and noisiness may be perceived as greater threats. Tanks are also less frequent in the study area and so may be more threatening through their unusualness.

An infrequently used route produced a higher probability of a response than a frequently used route, whilst controlling for distance from the stone curlew. This parameter only occurred in the vehicle active model. This suggests a degree of habituation to the most regularly used route at a site for vehicles. Vehicles are more likely to be on set, well defined tracks and it is easy for a route to become well known. Any deviation off a track is very unusual and so an increased probability of a response is observed due to this ‘surprise’ effect, particularly as the stone curlew can not easily predict the route that will be taken and must make the decision to react to the disturbance without knowing where the PDA will be headed. Additionally, although not significant in the models, vehicles on infrequently used routes were more likely to be tanks, which may have more risk associated with them.

If year was a factor in all models, this would suggest that the stone curlew response to distance can not be generalised. However, it does not seem to be an important parameter, and any effects are likely to be related to different individuals being measured between years. Julian date occurred as a minor significant effect in some models. The stone curlew breeding season is long (March-September) and the weak negative relationship between date and probability of a response is probably related to higher probabilities of a response associated with the egg and chick stages in the season, compared to the possibly less risky roosting and post breeding stage. Additionally, the negative relationship may be a slight indication of habituation to disturbance occurring within a season (Knight and Temple, 1986).

Predator size is likely to be correlated with risk (Ydenberg and Dill, 1986) and has been shown to positively correlate with response distances (e.g. Dill, 1974a, Hurley and Hartline, 1974). The reasoning is possibly that large groups are perceived to be more threatening, but may also be a result of increased visibility. Beale and Monaghan (2004) found that nest success of kittiwakes and guillemots was negatively related to ‘people load’, a combination parameter that included both the number of visitors per disturbance event with their distance from nests. In our study, the number of agents in a PDA event was found to have a significant effect, in addition to the presence of the PDA itself only in the model of alert behavioural responses of stone curlews to

vehicles. In this case the effect may be to do with noise. Large groups of military vehicles (>25) are common on Salisbury Plain Training Area and this may evoke a stronger alert response, however active response probability is not increased. This lack of association between PDA group size and response in other models may have been due to low statistical power because PDA group sizes greater than one were rare in our study.

Other factors not analysed in this study but potentially important when determining the risk of disturbance are the vulnerability of the eggs or chicks, accessibility to the nest site, weather and ambient temperature. Changes in nest defence with respect to all of issues have been observed (Montgomerie and Weatherhead, 1988). For example, parental response to disturbance may differ during extreme weather conditions because eggs can overheat and fail if left on the ground in the midday sun, and chicks may overheat or risk hypothermia in cold wet weather. Also for reasons to do with chick vulnerability, response may differ at different times of the day. Stone curlews may also show a lowered response if the nest site is inaccessible (for example if on a plot in a dense arable crop, or behind a fence).

Habituation

Animals often experience repeated stimuli in nature (Burger and Gochfield, 1990), and by constantly responding unnecessarily they risk wasting energy or suffer costs in other ways. Human disturbance has few direct effects on reproduction and by responding to human disturbance stimuli when the risk is low the birds may suffer. Therefore, habituation to disturbance has been observed (e.g. Burger and Gochfield, 1983, Ikuta and Blumstein, 2003). Habituation is demonstration that prey adjust their anti predator behaviour depending on circumstances and experience (Helfman, 1986) and may work because the stone curlew learns that the risk associated with a PDA type is low. However, habituation is perhaps better described as ‘variation in tolerance’ because ‘habituation’ suggests that human disturbance should not be a concern if birds can adapt. Many studies report that shyer individuals leave an area and fail to reproduce because they can not adapt to disturbance (Fowler, 1999).

I considered that habituation may occur depending on the disturbance event rates at a site and the age or experience of the breeding birds. In contrast to some studies (Lord *et al.*, 2001, Keller, 1989) but in common with others (Ellenberg *et al.*, 2006, Conomy *et al.*, 1998), disturbance levels at sites did not directly affect the probability of a response being observed. However, the age of the stone curlew had a negative relationship with the probability of a response. Younger birds

have an increased probability of responding in an alert way to vehicles, and an active way to people walking on foot. In particular, birds younger than three years (potential first time breeders) had an increased probability of becoming alert to vehicles.

Again, studies of nest defence can help explain responses. Experience in dealing with nest predators should result in changes in responses shown by individuals through their lifetimes (Montgomerie and Weatherhead, 1988). The perceived risk of the disturbance may decrease as parent stone curlews learn more about the capability of the PDA as a nest predator. If experience indicates that parents have no need to avoid a certain PDA type, then such large response are probably not necessary, and the observed habituation occurs. Stone curlews are long-lived and exhibit some degree of site-faithfulness; both of these characteristics give birds the opportunity to habituate through learning that humans are not realistic potential predators (Andersen, 1990, Lord *et al.*, 2001).

Gill *et al* (2001) stress that from a conservation perspective, human disturbance is only important if it affects survival or fecundity and causes a long term population decline. However, many disturbance studies extrapolate behavioural results and make recommendations for management of access based on behaviour and flight initiation distance. These recommendations usually involve buffer zones or set-back distances where disturbance is excluded within a certain distance (Rodgers and Schwikert, 2002, Richardson and Miller, 1997, Rodgers and Smith, 1995). However, the models presented in this chapter show that a stone curlew's behavioural response to disturbance varies as a function of many attributes to do with the PDA and the bird's ability to track changes in risk, and not just with distance. As a result, if management is to be based on behavioural measures it must take into account more than simply the flight initiation distance.

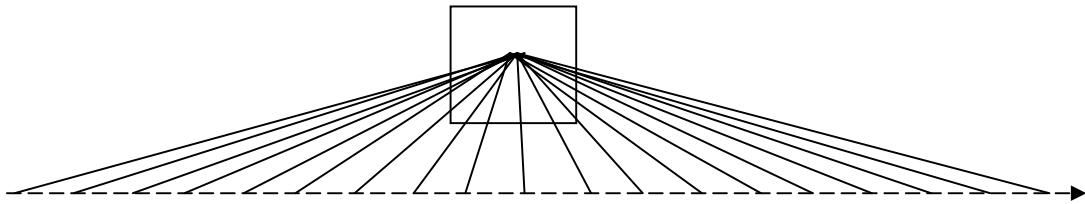
In the next chapter I use the new response per unit distance travelled modelling procedure to improve the disturbance event rate variable by deriving a new disturbance event rate which combines the frequency of disturbance with the behavioural response of the stone curlew to the specific PDA events I observed near stone curlew nesting sites. This new disturbance measure is then used to predict the wider implications of human disturbance on stone curlew use of breeding plots and breeding success (Chapters 6-8).



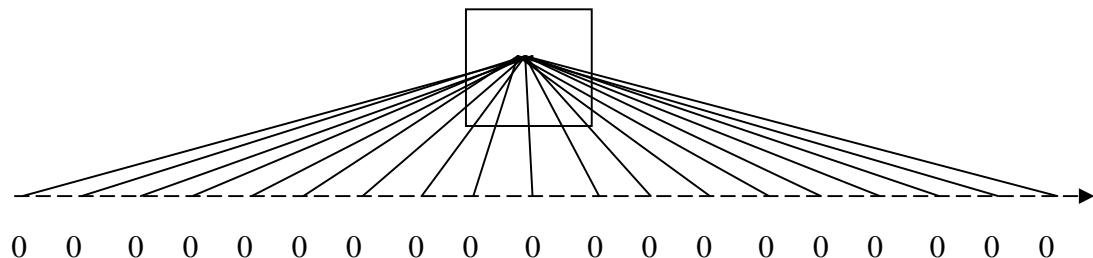
a) A PDA event (e.g. walker, vehicle) passes a stone curlew plot in the direction shown.



b) The route taken by the PDA is split into equal sections (e.g. mm).



c) As the PDA moves along the route, the distance between the PDA and the stone curlew plot is calculated for each mm section



d) The stone curlew has a chance to respond to the PDA at each point along the route and the probability of a response can be modelled as a function of distance between the stone curlew and the PDA and other explanatory variables. In this example the zeros represent no responses in any of the sections of the route. All of these chances to react can be used in the modelling process.

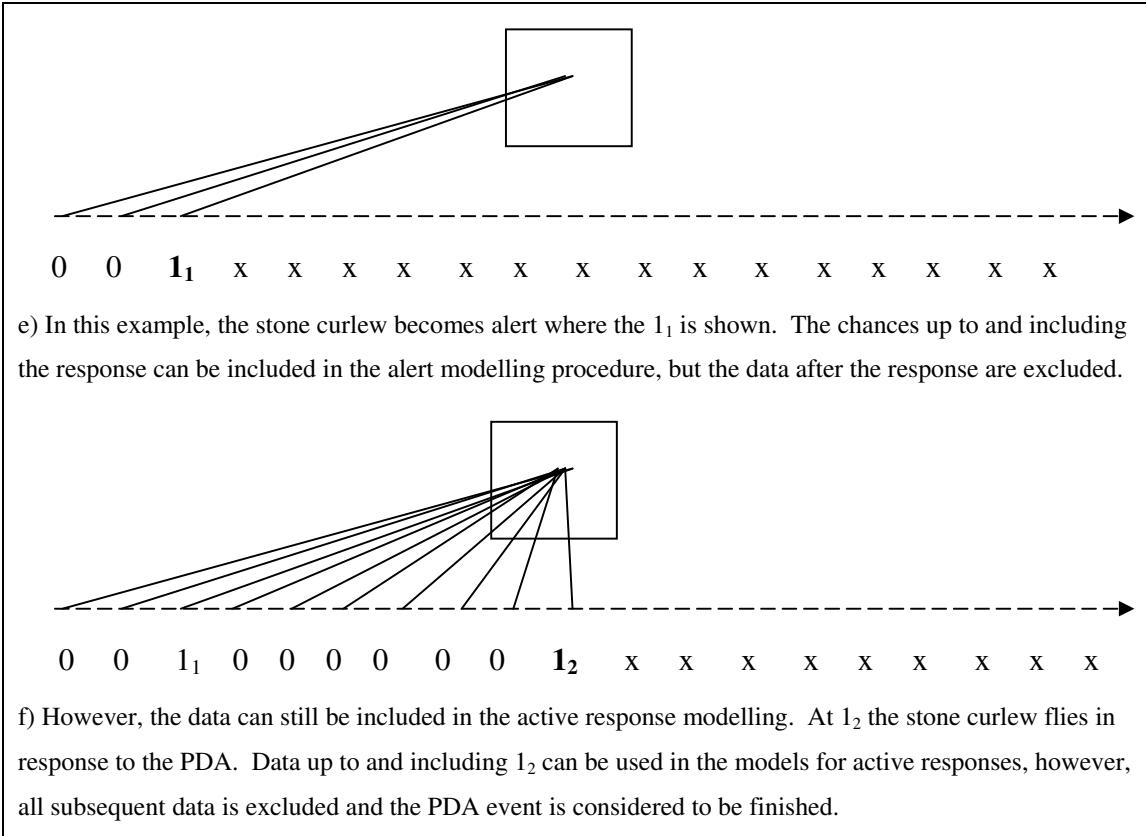


Figure 4.1. Diagram illustrating the principles underlying the modelling of stone curlew responses to disturbance. The units in the analysis are the sections of route. Independent variables, as listed in Table 4.1, can be attached to each of these, including the distance between the PDA and the bird.

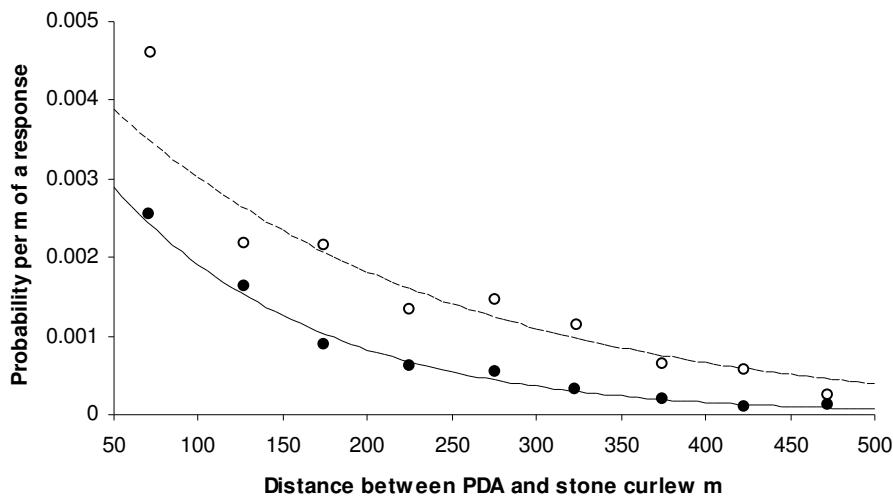


Figure 4.2. Probability per metre traversed of a response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are logistic regression models fitted to the disaggregated data. Models are shown separately for alert (◦---) and active responses (●—). Models were fitted in terms of probability per millimetre traversed, but probability per metre is shown for clarity.

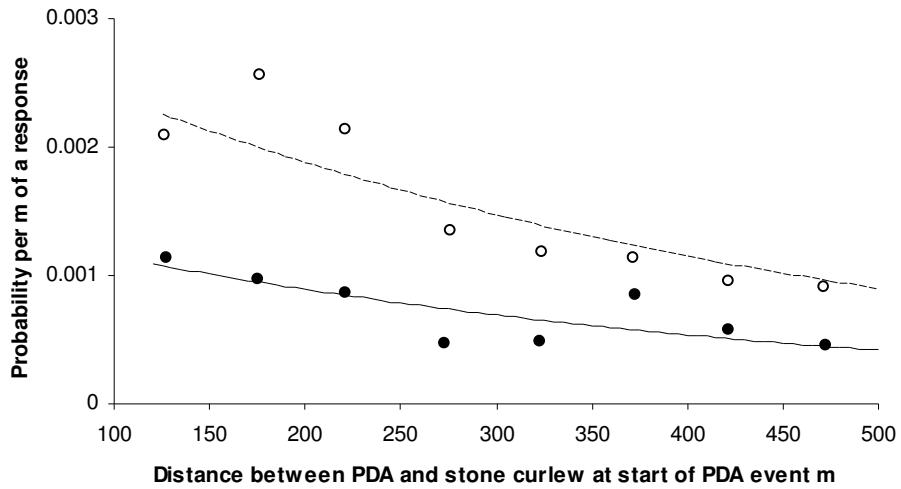


Figure 4.3. Probability per metre traversed of a response by a stone curlew to PDA events in relation to distance between the bird and the PDA when the PDA first becomes visible to the stone curlew. The points are for the proportion of active responses in distance bins and lines are logistic regression models fitted to the disaggregated data. Models are shown separately for alert (○---) and active responses (●—). Models were fitted in terms of probability per millimetre traversed, but probability per metre is shown for clarity.

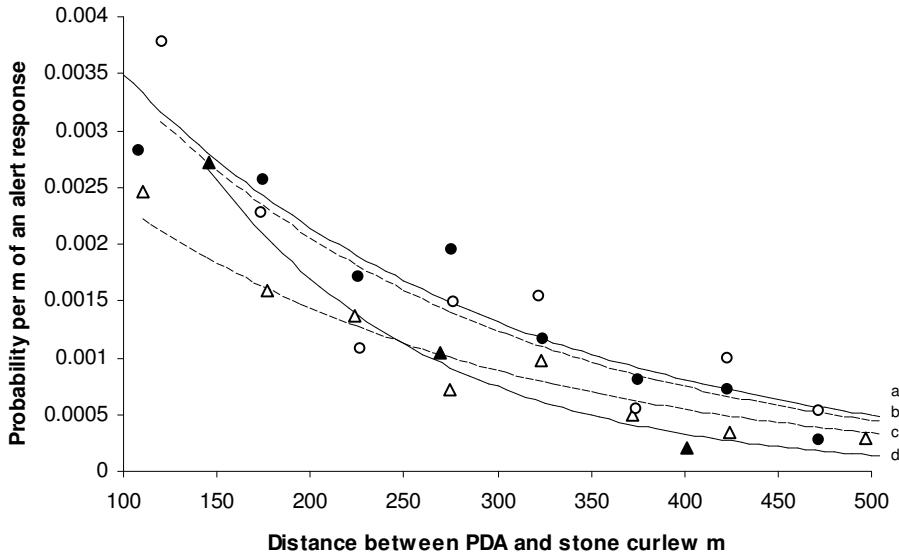


Figure 4.4. Probability per metre traversed of an alert response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for different stages of the breeding cycle and consider only the effect of distance: settlement (line c symbol Δ), egg (b \circ), chick (a \bullet), post failure (d \blacktriangle)

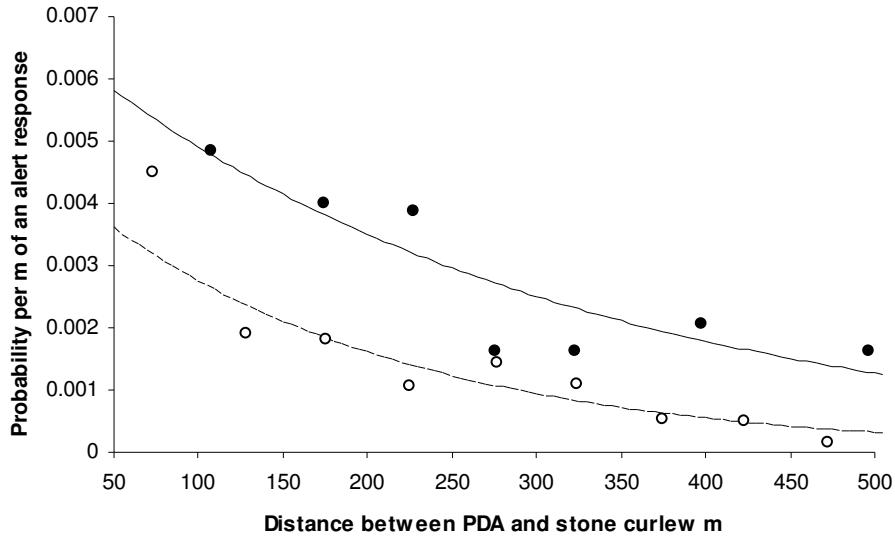


Figure 4.5. Probability per metre traversed of an alert response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for frequently used (◦---) and infrequently used routes (● –) and consider only the effect of distance.

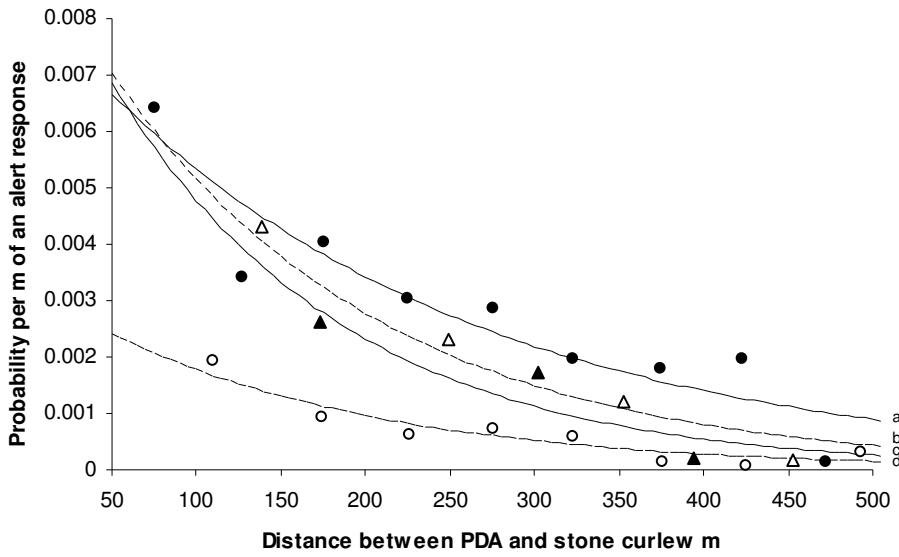


Figure 4.6. Probability per metre traversed of an alert response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for different PDA types and consider only the effect of distance: people on foot (a ●), joggers (b Δ), vehicles (d ○), other (c ▲).

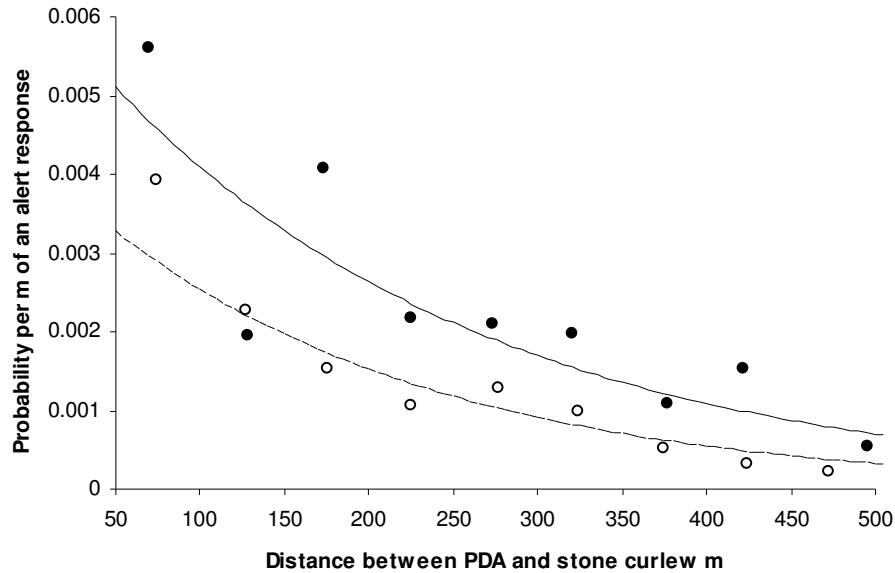


Figure 4.7. Probability per metre traversed of an alert response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for 2004 (◦---) and 2005 (●—) and consider only the effect of distance.

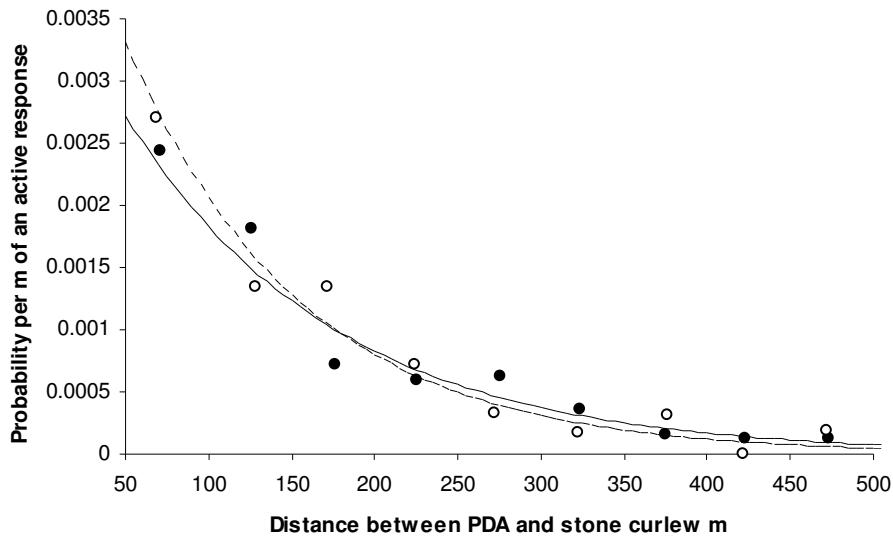


Figure 4.8. Probability per metre traversed of an active response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for 2004 (◦---) and 2005 (●—) and consider only the effect of distance.

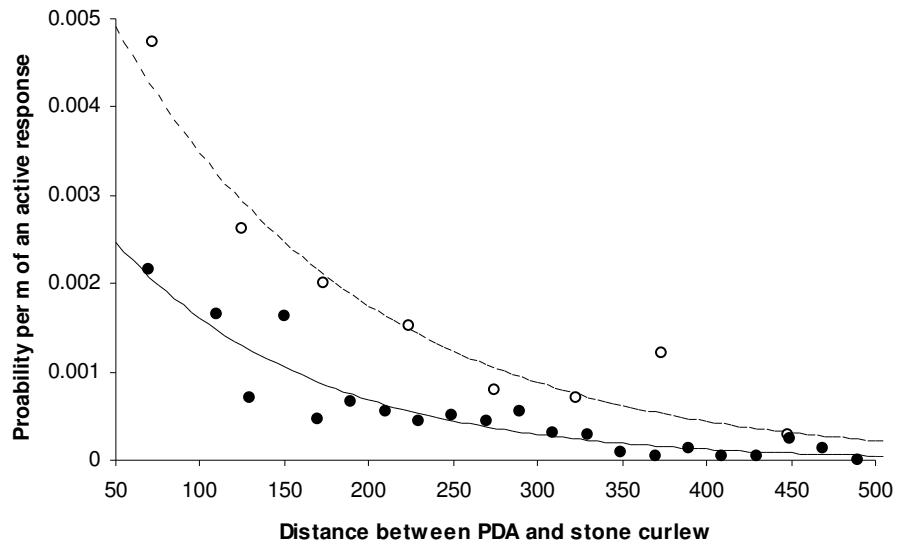


Figure 4.9. Probability per metre traversed of an active response (running or flying) by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for an infrequently (○---) and frequently (●—) used routes and consider only the effect of distance.

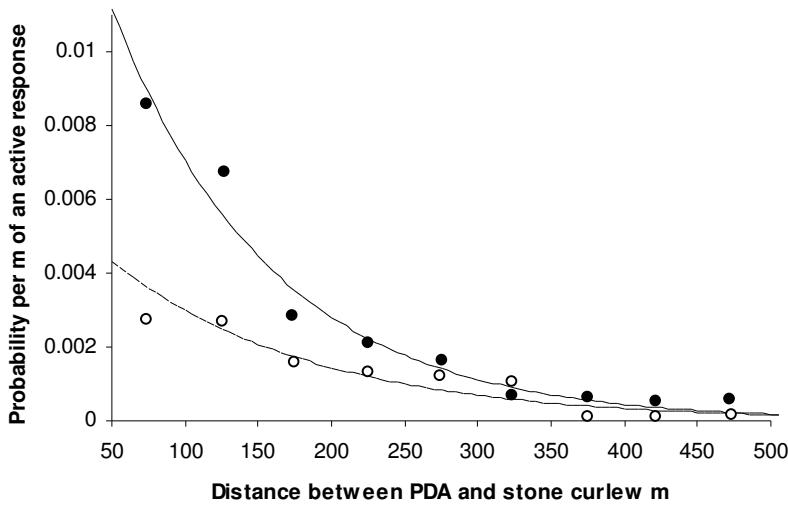


Figure 4.10. Probability per metre traversed of an active response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for without dogs (---) and with dogs (● —) and consider only the effect of distance.

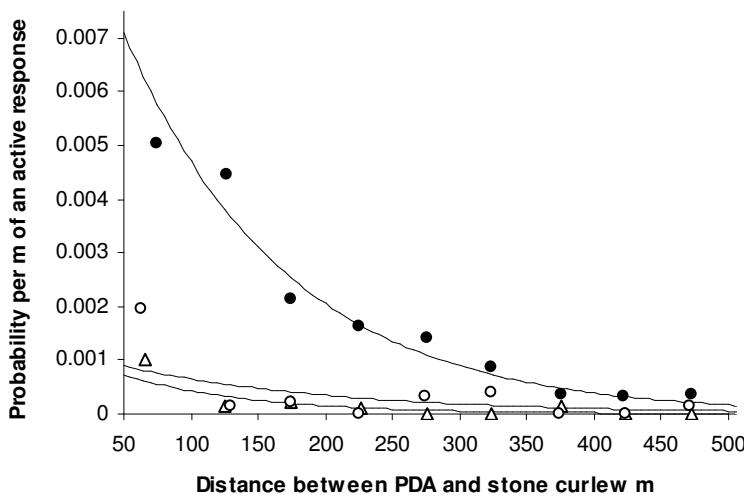


Figure 4.11. Probability per metre traversed of an active response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for people walking on foot (● —), vehicles (Δ—) and other types of PDA (---) and consider only the effect of distance.

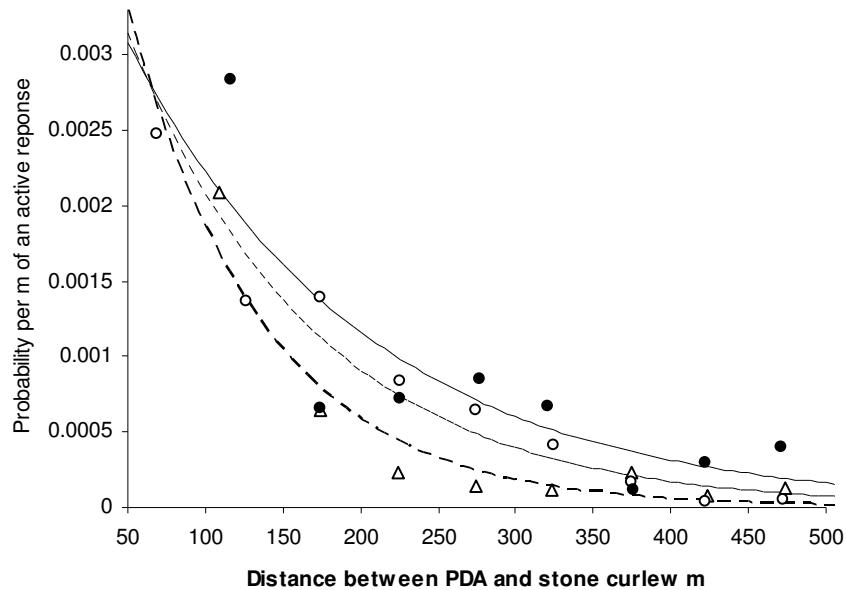


Figure 4.12. Probability per metre traversed of an active response by a stone curlew to PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for the chick (●), egg (○---) and settlement (Δ---) stages of the breeding cycle and consider only the effect of distance.

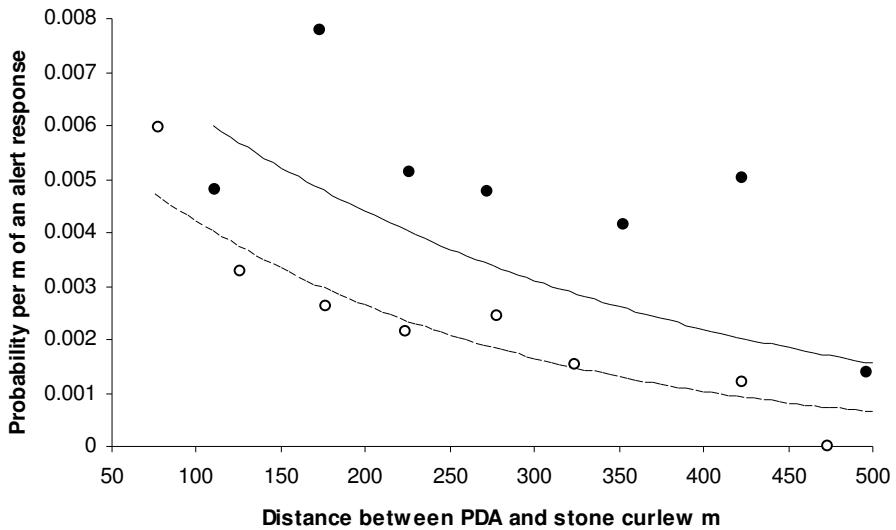


Figure 4.13. Probability per metre traversed of an alert response by a stone curlew to people on foot PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for 2004 (◦---) and 2005 (●—) and consider only the effect of distance

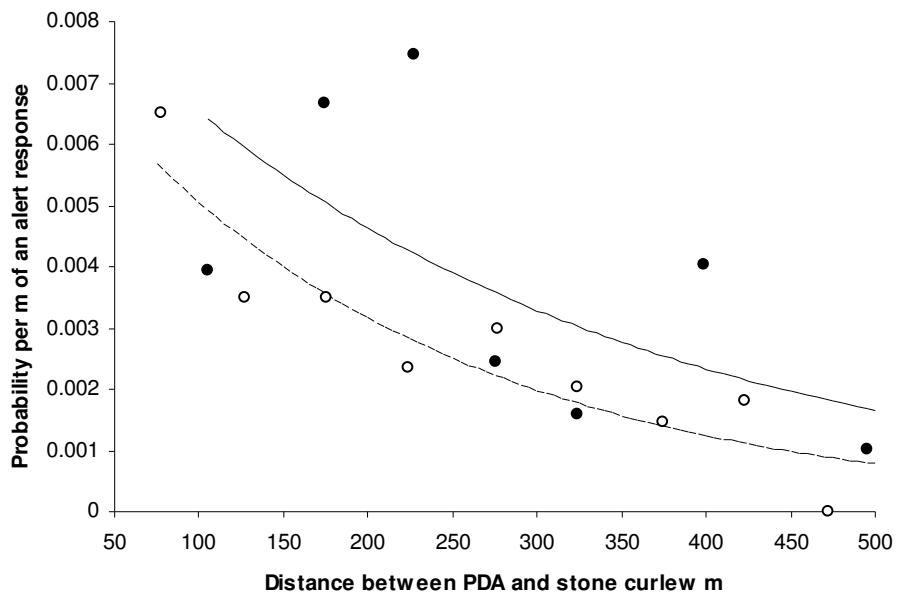


Figure 4.14. Probability per metre traversed of an alert response by a stone curlew to people on foot PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for frequently used (◦---) and infrequently used routes (●—) and consider only the effect of distance

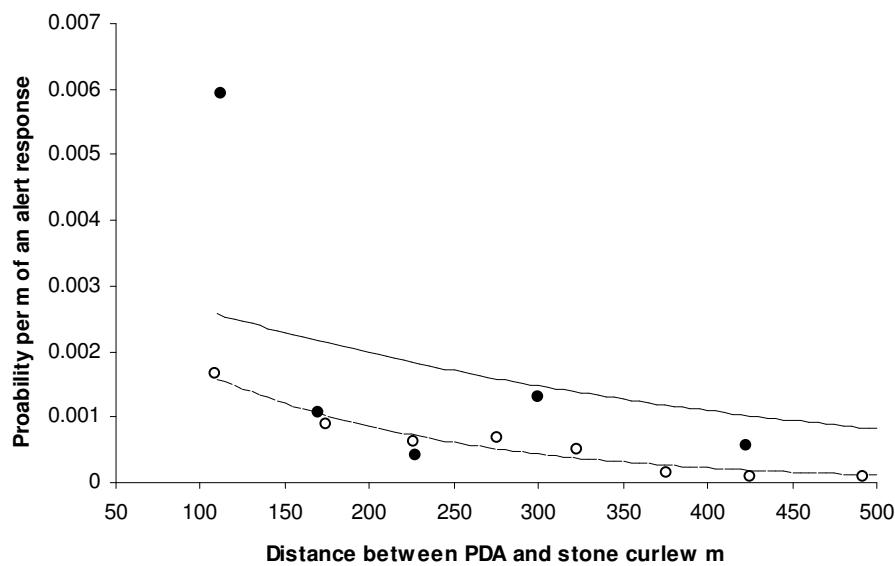


Figure 4.15. Probability per metre traversed of an alert response by a stone curlew to vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for frequently used (○---) and infrequently used routes (● –) and consider only the effect of distance.

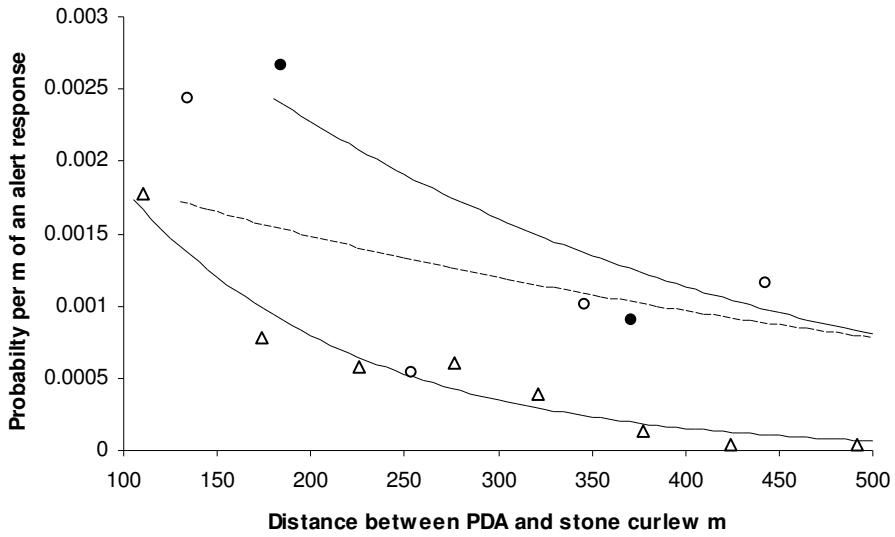


Figure 4.16. Probability per metre traversed of an alert response by a stone curlew to vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for motorbikes (●—), tanks (○---) and normal vehicles (Δ —) and consider only the effect of distance.

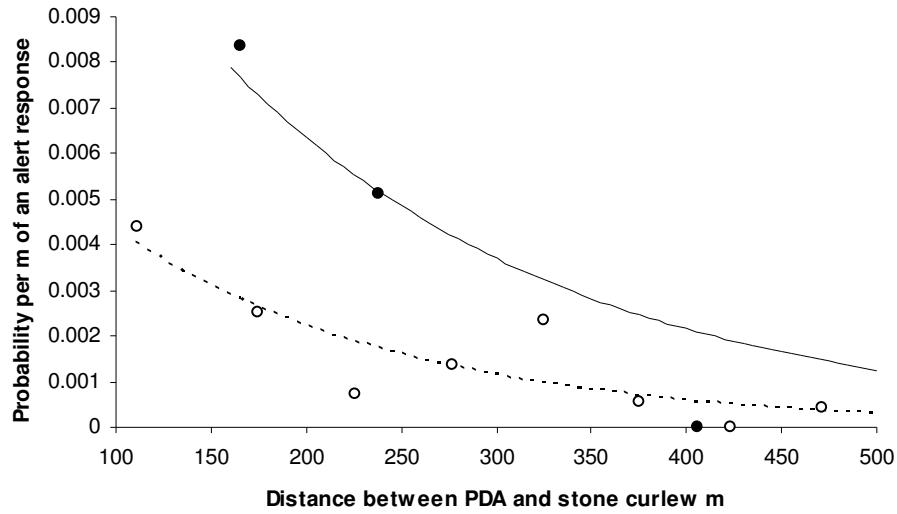


Figure 4.17. Probability per metre traversed of an alert response by a stone curlew to other types of PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for infrequently used (● –) and frequently used routes (○---) and consider only the effect of distance.

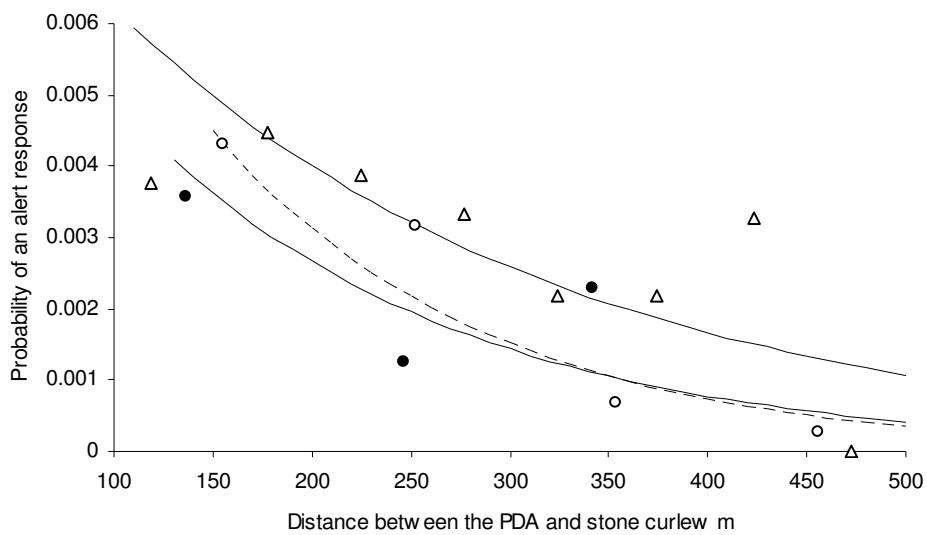


Figure 4.18. Probability per metre traversed of an alert response by a stone curlew to non vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for cyclists (●—), joggers (○---) and people walking on foot (Δ—) and consider only the effect of distance.

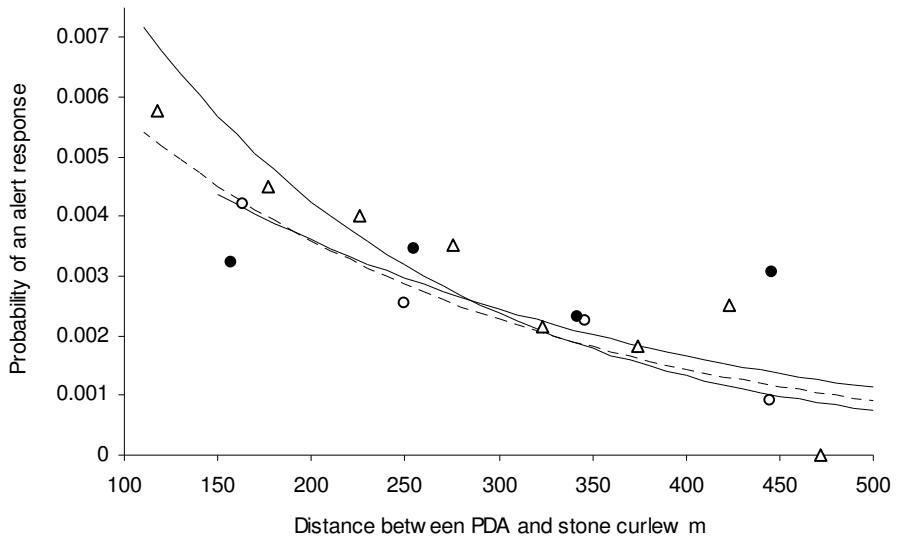


Figure 4.19. Probability per metre traversed of an alert response by a stone curlew to non vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for the chick (●—), settlement (○---) and egg (Δ—) stages of the breeding cycle and consider only the effect of distance.

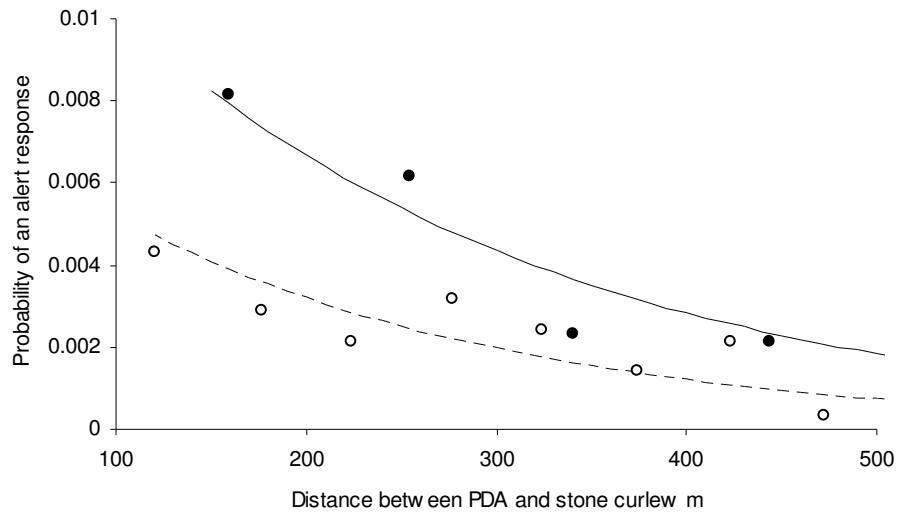


Figure 4.20. Probability per metre traversed of an alert response by a stone curlew to non vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of alert responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for frequently used (◦---) and infrequently used routes (●—) and consider only the effect of distance.

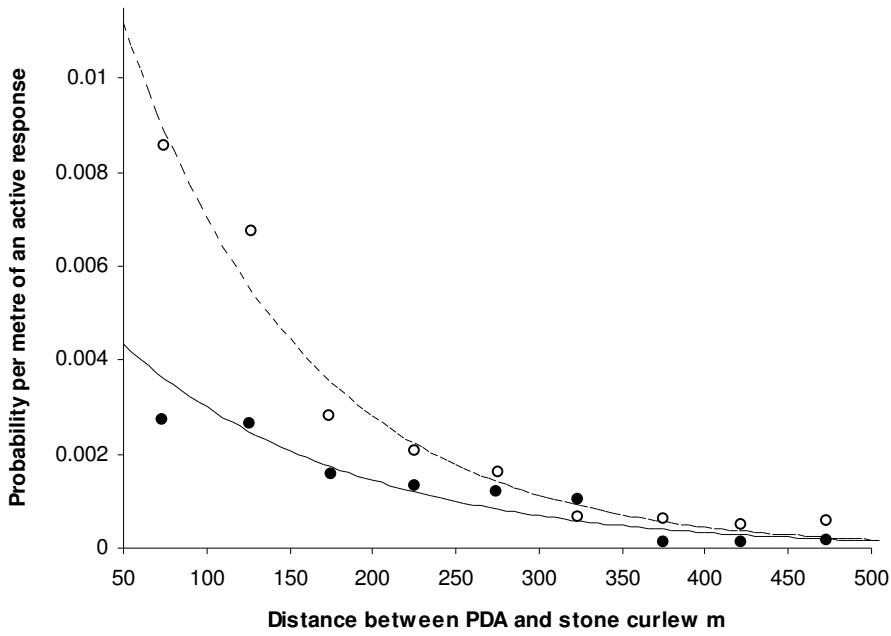


Figure 4.21. Probability per metre traversed of an active response by a stone curlew to people on foot PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for people without (● –) and with (○---) dogs and consider only the effect of distance.

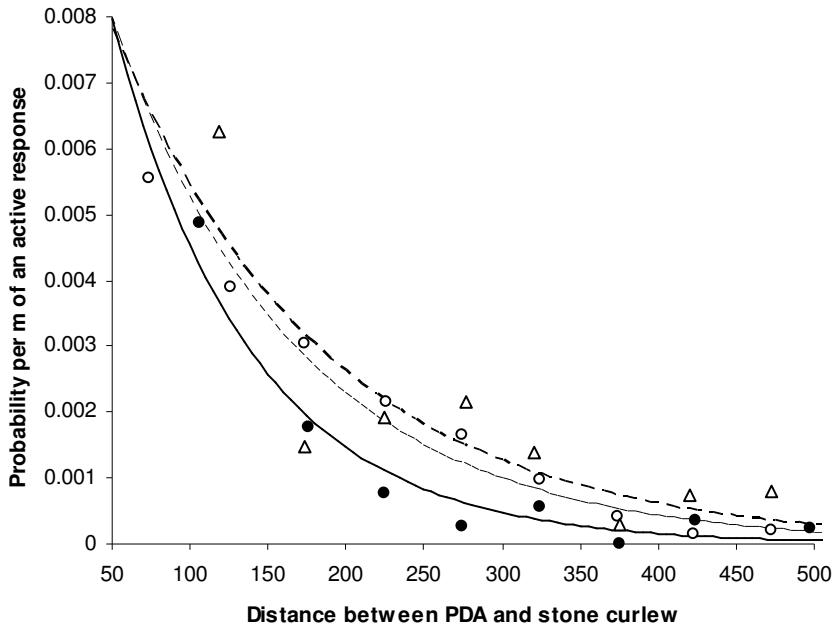


Figure 4.22. Probability per metre traversed of an active response by a stone curlew to people on foot PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for the chick (Δ)—, egg (○---) and settlement (●)– stages in the breeding cycle and consider only the effect of distance.

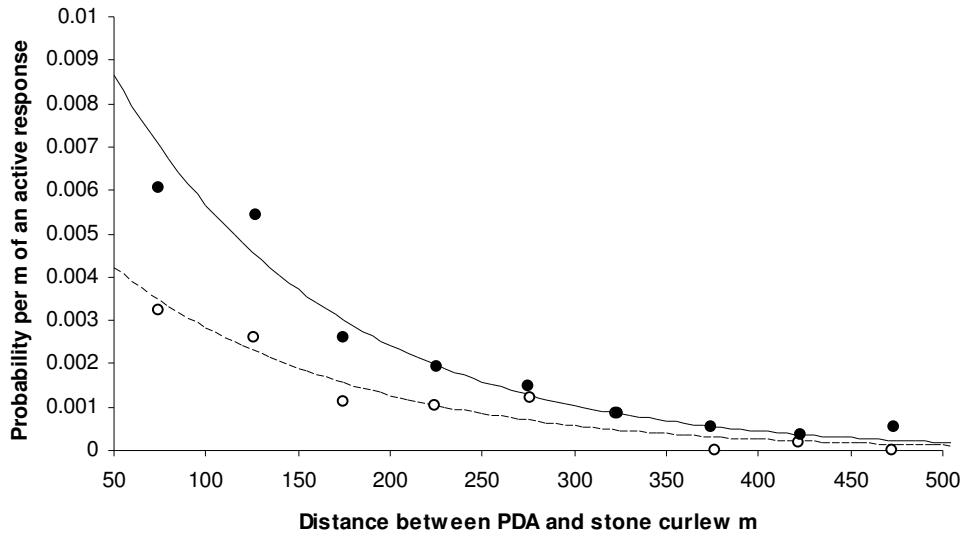


Figure 4.23. Probability per metre traversed of an active response by a stone curlew to people on foot PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for when the PDA is heading directly towards (● –) or directly away (○---) from the stone curlew and consider only the effect of distance.

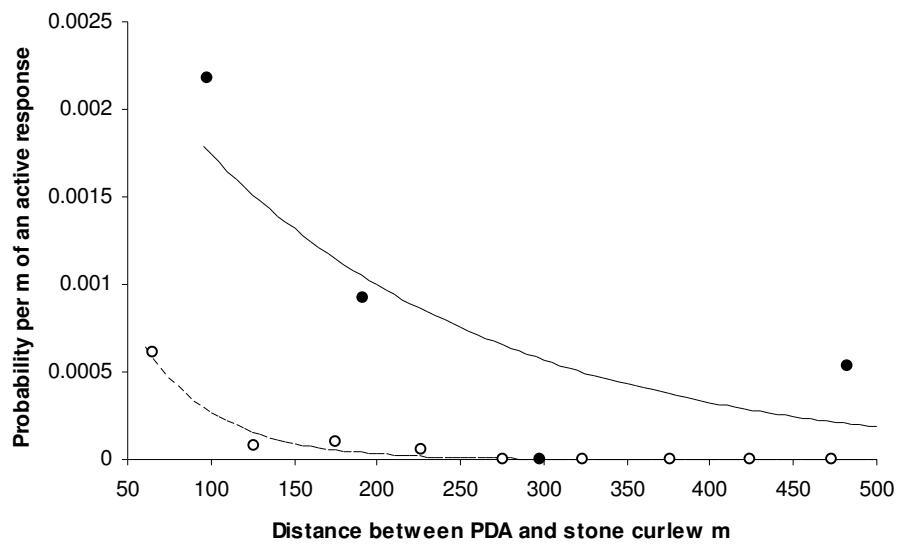


Figure 4.24. Probability per metre traversed of an active response by a stone curlew to vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for infrequently (\bullet —) and frequently used routes (\circ ---) and consider only the effect of distance.

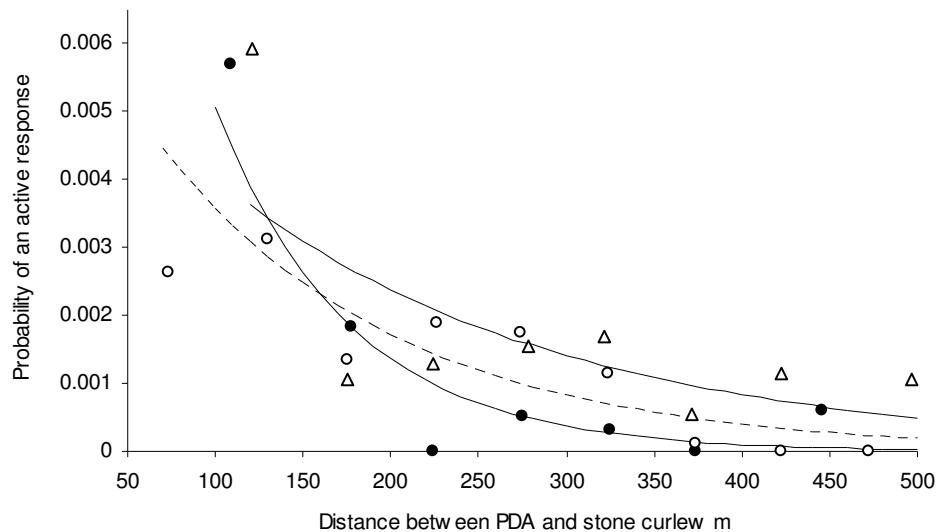


Figure 4.25. Probability per metre traversed of an active response by a stone curlew to non vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for the chick (Δ —), egg (○---) and settlement (●—) stages in the breeding cycle and consider only the effect of distance.

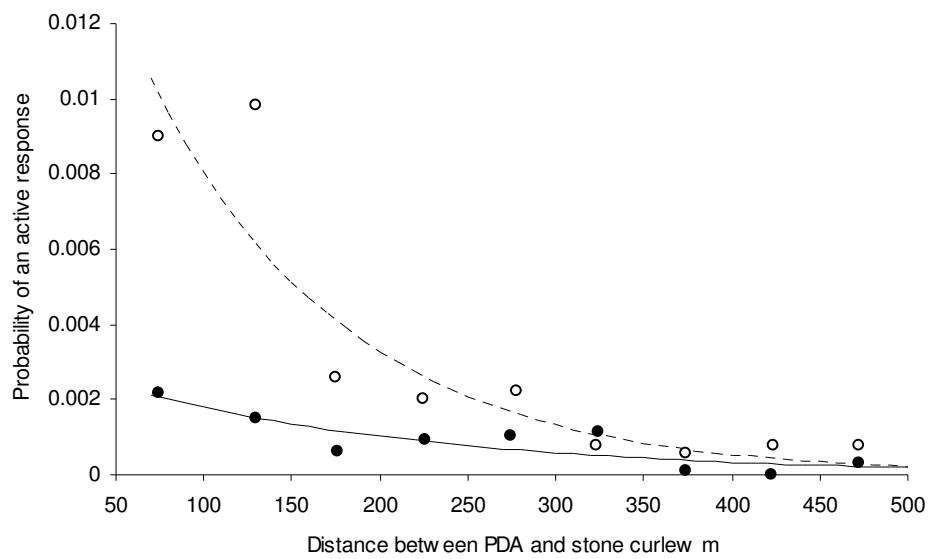


Figure 4.26. Probability per metre traversed of an active response by a stone curlew to non vehicle PDA events in relation to distance between the bird and the PDA. The points are for the proportion of active responses in distance bins and lines are fitted logistic regression models. Models were fitted separately for people without (● –) and with (○---) dogs and consider only the effect of distance.

Table 4.1. Candidate variables used in the logistic regression models

Candidate explanatory variables	Type of variable	Factor levels
Year	Factor	2004, 2005
Frequently used route	Factor	At each sites the most frequently used route was defined based on observations of PDA events
Stage of breeding	Factor	Settlement Egg Chick Post Failure Roost Single bird
PDA type	Factor	Subdivisions of PDA type used in full MAMs only: People walking on foot Jogger Cyclist Horse rider Vehicle (all types)
		Subdivisions of vehicle type used in vehicle MAMs only: Normal vehicle (non tank) Tank Motorbike
		Subdivisions of PDA type used in ‘other’ MAMs only: Jogger Cyclist Horse rider
		Subdivisions of PDA type used in non vehicle MAMs only: People walking on foot Jogger Cyclist Horse rider
Presence of dog	Factor	Dog No dog Factor not present in vehicle models
Julian date	Continuous	
Total agents	Continuous	
Speed side to side	Continuous	
Speed to fro	Continuous	
Start distance	Continuous	
Distance between PDA and stone curlew	Continuous	

Table 4.2. Parameter estimates from a logistic regression model relating the probability of an **alert** response of a stone curlew per mm of route taken by PDA events to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is settlement for stage).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 2753.73 with 12933 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-10.9600			
Year	0.4365	18.51	1	0.000016
Julian date	-0.004092	6.57	1	0.010
Frequently used	-0.5240	19.41	1	0.000010
Stage		13.89	5	0.016
Settlement	0			
Egg	0.2542			
Chick	0.5639			
Post failure	0.1946			
Roost	-0.09001472			
Single bird	0.4631			
PDA type		30.37	3	<.00001
People walking on foot	0			
Joggers	-0.1666			
Vehicles	-0.8802			
Other	-0.3092			
Total agents	0.07233	10.02	1	0.0015
Speed side	-0.00001936	18.41	1	0.000017
Speed to fro	0.000009523	16.98	1	0.000037
Distance to PDA	-0.0050000	354.59	1	<0.00001
Dog		0.89	1	0.346
Start distance		0.45	1	0.495

Table 4.3. Parameter estimates from a logistic regression model relating the probability of an **active** response of a stone curlew per mm of route taken by PDA events to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is settlement for stage).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 2199.29 with 19870 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-10.6449			
Year	-0.3533	23.67	1	<0.00001
Julian date	-0.005045	6.54	1	0.010
Frequently used route	-0.5915	19.97	1	<0.00001
Stage		22.87	5	0.00035
Settlement	0			
Egg	0.4285			
Chick	0.6802			
Post failure	-0.1815			
Roost	-0.2877			
Single bird	1.3951			
PDA type		33.97	2	<0.00001
People on foot	0			
Vehicles	-0.9411			
Other	-1.2006			
Speed side	-0.00005223	26.37	1	<0.00001
Speed to fro	0.00001205	6.43	1	0.011
Dog	0.8132	43.68	1	<0.00001
Distance to PDA	-0.008741	429.05	1	<0.00001
Start distance		0.95	1	0.327
Total agents		0.876	1	0.345

Table 4.4. . Parameter estimates from a logistic regression model relating the probability of an **alert** response of a stone curlew per mm of route taken by person on foot PDA events to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 1654.39 with 8917 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-11.7222			
Year	0.7935	37.82	1	<0.00001
Frequently used route	-0.3662	5.93	1	0.014
Distance to PDA	-0.004247	168.35	1	<0.00001
Speed side		2.57	1	0.105
Stage		3.98	4	0.404
Julian Date		0.99	1	0.317
Total agents		0.59	1	0.434
Speed to fro		0.19	1	0.666
Start distance		2.90	1	0.0883
Dog		0.47	1	0.485

Table 4.5. Parameter estimates from a logistic regression model relating the probability of an **alert** response of a Stone curlew per mm of route taken by motor vehicles to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 686.47 with 2045 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-11.7531			
Frequently used route	-0.5206	4.93	1	0.026
PDA type		10.74	2	0.0046
Normal vehicle	0			
Tank	0.5480			
Motorbike	0.8117			
Speed side	-0.00002011	17.96	1	0.000022
Distance to PDA	-0.005187	48.29	1	<0.00001
Total agents	0.06089	6.83	1	0.0089
Speed to fro	0.000009728	15.71	1	0.000073
Start distance	-0.001119	4.53	1	0.033
Stage		7.37	5	0.195
Year		0.18	1	0.674
Julian date		1.43	1	0.236

Table 4.6. Parameter estimates from a logistic regression model relating the probability of an **alert** response of a stone curlew per mm of route taken by other types of PDA to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 386.61 with 1969 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-8.7309			
Julian date	-0.005703	3.93	1	0.047
Frequently used route	-1.1669	12.62	1	0.00038
Speed to fro	0.000033349	4.16	1	0.041
Distance to PDA	-0.006390	80.54	1	<0.00001
Stage		2.49	4	0.646
Year		1.87	1	0.175
Total agents		0.75	1	0.385
Speed side		0.29	1	0.589
Start distance		1.35	1	0.245
PDA type		0.25	2	0.877

Table 4.7. Parameter estimates from a logistic regression model relating the probability of an alert response of a stone curlew per mm of route taken by non vehicle PDA events to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 1878.26 with 10883 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-10.7943			
Year	-1.1932	52.20	1	<0.00001
Disturbance type:		17.58	3	0.00053
People walking on foot	0			
Joggers	-0.3373			
Cyclists	-0.8936			
Horse riders	-0.6350			
Frequently used route	-0.7275	26.75	1	<0.00001
Distance to PDA	-0.004956	239.48	1	<0.00001
Stage:		154.99	4	<0.00001
Settlement	0			
Egg	0.8693			
Chick	1.4739			
Post failure	-5.9414			
Roost	-6.6054			
Julian Date	-0.005217	15.71	1	0.000073
Speed side		0.14	1	0.707
Total agents		0.15	1	0.695
Speed to fro		0.87	1	0.354
Start distance		0.74	1	0.387
Dog		3.31	1	0.068

Table 4.8. Parameter estimates from a logistic regression model relating the probability of an active response of a stone curlew per mm of route taken by a person walking on foot to distance between the stone curlew and PDA event, speed directly towards or away, presence of dog (factor), and stage in breeding season (factor, 5 levels). Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 1787.34 with 14110 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-12.1015			
Stage		25.62	4	<0.0001
Settlement	0			
Egg	0.41015			
Chick	0.4979			
Post failure	-0.5115			
Roost post breeding	-0.5909			
Presence of dog (Factor)	0.6931	31.83	1	<0.0001
Speed to fro	0.00006081	12.80	1	0.0003470
Distance to PDA	-0.008825	361.42	1	<0.0001
Year		2.32	1	0.141
Julian date		0.89	1	0.332
Frequently used route		3.10	1	0.0559
Total agents		2.30	1	0.135
Speed side		0.05	1	0.943
Start distance		0.20	1	0.579

Table 4.9. Parameter estimates from a logistic regression model relating the active response of a stone curlew per mm of route taken by motor vehicle PDA events to distance between the stone curlew and PDA event, speed in a sideways direction, and route (factor, 2 levels). Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM.. The residual deviance of the model is 210.23 on 2648 degrees of freedom.

The table also shows the *p* value from the bootstrap estimates described in section 4.7.

	Parameter estimates	Reduction in residual deviance	df	p	p value from bootstrap
Intercept	-10.7985				
Frequently used route	-2.3248	41.83	1	<0.0001	0.002
Speed side	-0.00005615	23.36	1	<0.0001	0.001
Distance to PDA	-0.009353	47.96	1	<0.0001	<0.0001
Stage		3.19	5	0.67	0.52
Year		0.27	1	0.59	0.24
Julian Date		1.62	1	0.20	0.15
Total agents		0.14	1	0.70	0.32
Speed to fro		1.68	1	0.19	0.28
Start distance		0.11	1	0.73	0.65
PDA type		4.95	2	0.083	0.06

Table 4.10. Parameter estimates from a logistic regression model relating the probability of an active response of a stone curlew per mm of route taken by other types of PDA (joggers, horse and cyclists) to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 166.67 with 3109 degrees of freedom.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	-14.4069			
Total agents	0.9413	4.70	1	0.030
PDA type		12.39	2	0.0020
Joggers	0			
Cyclists	-1.7162			
Horse riders	-2.4594			
Distance to PDA	-0.006286	20.17	1	0.00000070
Speed to fro	0.00007052	5.70	1	0.016
Route		2.51	1	0.115
Stage		1.67	5	0.794
Julian date		0.98	1	0.326
Year		2.27	1	0.137
Speed side		0.018	1	0.898
Start distance		1.77	1	0.183

Table 4.11. Parameter estimates from a logistic regression model relating the probability of an active response of a stone curlew per mm of route taken by non vehicle PDA events to explanatory variables. Coefficients for categorical variables represent the difference in the log-odds of a response between a particular category and the reference category (e.g. the reference category is route in the intercept).

Variables included in the MAM are shown in bold. For those variables, changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for the effect of deleting each variable from the MAM. For non-significant variables, the equivalent statistics are shown for the effects of adding them, singly, into the MAM. The residual deviance of the model is 1878.26 with 10883 degrees of freedom.

The table also shows the *p* value from the bootstrap estimates described in section 4.7. For the multi-level factors of stage and disturbance type, the most significant bootstrap estimate *p* value is shown.

	Parameter estimates	Reduction in residual deviance	df	<i>p</i>	<i>p</i> value from bootstrap
Intercept	-12.2067				
Stage		27.51	4	<0.0001	0.002
Settlement	0				
Egg	0.4290				
Chick	0.5196				
Post failure	-0.4706				
Roost post breeding	-0.6022				
Disturbance type		58.42	3	<0.0001	0.001
People on foot	0				
Joggers	-1.1104				
Horse riders	-1.6448				
Cyclists	-2.8338				
Presence of dog	0.7674	39.49	1	<0.0001	0.001
Speed to fro/metres per hour	0.00006135	17.46		<0.0001	<0.001
Distance to PDA/metres	-0.008591	395.78	1	<0.0001	<0.001
Year		3.23	1	0.0767	0.06
Julian date		0.75	1	0.385	0.28
Total agents		3.71	1	0.0543	0.06
Speed side		0.01	1	0.923	0.75
Start distance		0.63	1	0.435	0.30
Frequently used route		1.78	1	0.177	0.15

Table 4.12. Summary of MAMs. Shown are the strengths and directions of relationships at the 0.05, 0.01 and 0.001 level. Light grey shading signifies that the variable was not present in the final MAM. Dark grey shading signifies that the parameter was not tested in this model.

Parameter	Model									
	Full		People walking on foot only		Vehicles only		Other PDAs only		Non vehicles	
	Alert	Active	Alert	Active	Alert	Active	Alert	Active	Alert	Active
Distance	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Frequently used route	- - -	- - -	-		-	- - -	- - -	- - -	- - -	
PDA type	***	***			**			**	***	***
Speed to fro	+++	+		+++	+++		+	+		+++
Year	+++	- - -	+++						- - -	
Speed side to side	- - -	- - -			- - -	- - -				
Dog		+++		+++						+++
Julian date	-	-					-		- - -	
Stage	*	***		***					***	***
Total agents	++				++			+		
Start distance					-					

Table 4.13. Effect of age of stone curlew, treated as a continuous variable, when added to the MAM selected earlier in the chapter. These analyses only use data for which the bird's age was known, which is fewer observations than used to select the MAM. Reduction in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown. The direction of the effect is denoted by + and - and its significance by (+), P > 0.05, + P < 0.05, ++ P < 0.01, +++ P < 0.001.

Model	Direction of effect of age	Reduction in deviance	df	p
People walking on foot alert		1.64	1	0.194
Vehicles alert	- - -	15.32	1	0.000090
Others alert		3.74	1	0.0524
Non vehicles alert	- - -	6.71	1	0.0095
People walking on foot active	- - -	5.80	1	0.015
Vehicles active		0.13	1	0.712
Non vehicles active	- - -	8.49	1	0.0035

Table 4.14. Effect of age of stone curlew, treated as categorical variable with one and two year old adults as one category and older birds as the other, when added to the MAM selected earlier in the chapter. These analyses only use data for which the bird's age was known, which is fewer observations than used to select the MAM. Reduction in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown.

Model	Reduction in deviance	df	p
People walking on foot alert	2.8575	1	0.090
Vehicles alert	15.1812	1	0.0000977
Others alert	1.1162	1	0.290
Non vehicles alert	0.6028	1	0.437
People walking on foot active	1.0789	1	0.299
Vehicles active	0.1690	1	0.681
Non vehicles active	5.7457	1	0.0165

Table 4.15. The effect of disturbance levels on response when added to the MAMs selected earlier in the chapter. These analyses only use data for which the average disturbance level at a site was known, which is fewer observations than used to select the MAM. Reduction in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown.

Model	Reduction in deviance	df	p
People walking on foot alert	0.18	1	0.666
Vehicles alert	2.10	1	0.145
Others alert	0.036	1	0.847
Non vehicles alert	0.47	1	0.493
People walking on foot active	0.0012	1	0.975
Vehicles active	0.040	1	0.844
Others active	1.075	1	0.298
Non vehicles active	2.14	1	0.145

5 Using models of behavioural responses to disturbance to improve the effectiveness of disturbance data

5.1 Summary

Potential disturbance events have many attributes that influence whether or not stone curlews show a behavioural response. In addition to distance between the potential disturbance agent (PDA) and the stone curlew, the probability of an active response to non motor vehicle PDA events is influenced by disturbance type, stage of breeding, presence of a dog and how quickly the PDA is moving towards the bird. Probabilities of responses to motor vehicle PDA events vary with route taken and side-to-side speed as well as distance between the PDA and the stone curlew. Models that describe the probability of an active response can be used to convert mapped data on the disturbance event into a predicted probability of responding. The calculation of the expected number of active response per unit time from mapped disturbance frequency data, then gives a measure of disturbance that effectively takes into account variation in PDA types and routes. This is preferable to a simple disturbance event rate which includes PDAs approaching the site within a specified distance.

5.2 Introduction

When comparing effects of disturbance between sites, crude event rates are usually used (e.g. Mallord, 2005, Liley, 1999, Taylor, 2002, and previous chapters in this thesis). This is the mean rate at which potential disturbance events occur per unit time within a set area. Whilst this sort of measure has been effective in explaining variation in breeding success and distribution in several species (Burger, 1991, Liley, 1999, Mallord, 2005), the method does not take into account the attributes associated with the disturbance (e.g. the distance between the bird and the PDA, type of PDA, speed, group size etc) and therefore the way in which a species responds to the level of risk (See Chapter 4). As a result, using a simple event rate, sites with high frequency of events involving motor vehicles are classed as highly disturbed, but stone curlews show a lower probability of response to vehicles than people on foot, so this is misleading. Attempts have been made to give ‘weightings’ to different types of disturbance which may or may not reflect the true level of risk to birds (e.g. Miller *et al.*, 1998), however, these weightings, unless based on observed behaviour, are arbitrary and difficult to justify.

In this chapter, I describe a new measure of disturbance event rate at which I use the same modelling approach as in Chapter 4 to produce an estimated *rate at which active responses would be expected to occur*, given the frequency, type of PDA, route of PDA and other attributes of the observed PDA events. It is then suggested that this variable can replace the use of disturbance event rates in subsequent analyses of stone curlew breeding success and distribution (Chapters 6-8).

5.3 Aims of Chapter

In this chapter I use all behavioural data collected over two years to:

- 5) Describe how the regression models selected in Chapter 4 can be used to convert mapped data on a PDA event into an expected probability of a response to the disturbance event. This can be done for sites with and without stone curlews present, provided that disturbance data has been collected.
- 6) Test the performance of the models in predicting responses to PDAs.
- 7) Describe how the modelled probabilities of a response can be combined to produce the expected number of active response per unit time at a site.

5.4 Model selection and analysis

The probability of a behavioural response by the stone curlew per section of route travelled can be modelled as a function of the variables measured for each PDA event (Table 2.1), by treating responses as binary response variables and following the analysis methods in Chapter 4. The variables in Table 4.1 were used to fit Minimal Adequate Models (MAMs) to model the probability of occurrence of an active response using logistic regression with a backwards-elimination model selection procedure (Crawley, 2002). MAMs were presented in Chapter 4, describing the probabilities of active and alert responses to:

1. All types of PDA
2. Motor vehicle PDAs
3. People walking on foot PDAs
4. Jogger, cyclist and horserider PDAs
5. Non motor vehicle PDAs

I selected two models to use to convert mapped data on a PDA event to an expected probability of a response to the disturbance event: the model describing the probability of an active response to a motor vehicle (Table 4.9) and the model describing the probability of an active response to a

non motor vehicle (Table 4.11). These two models used all the data I had collected over two years. The active response was used as it is probably of more concern to stone curlews for the reasons already discussed (Chapters 3 and 4).

These two MAMs (summarised in Table 5.1) were used to calculate the expected probability of response to PDA events at sites with and without stone curlews. The performance of the fitted MAMs in predicting a response or lack of response to mapped PDA events, was assessed using receiver operating characteristic (ROC) curves (Osborne *et al*, 2001). This is a superior approach to some methods used which predict that a response will occur if the modelled probability of occurrence exceeds 0.5 or some arbitrary probability. The ROC curve is constructed by varying the cut-off point that determines which modelled probabilities are assumed to be the threshold level for a response and plotting the sensitivity against 1-specificity (Figure 5.1). Sensitivity is the probability that a positive result will be correctly identified as positive by the model (e.g. a stone curlew responding to a PDA event). Sensitivity is calculated by the number of true positives divided by the sum of the number of true positives plus the number of false negatives. Specificity is the probability that a negative result will be correctly identified as being negative (e.g. a stone curlew *not* responding to a PDA event) and is calculated by number of true negatives divided by the sum of the number of true negatives plus the number of false positives. A sensitivity and specificity of 100% means that all cases are correctly categorised as being positive or negative. If the model was no better than chance at predicting a positive event, the plot would show a line following the positive diagonal (Figure 5.1). However, the fit of a model with a better than chance performance will follow a line occupying the upper left half of the chart. The area under the ROC curve (AUC) is a measure of overall fit, varying from 0.5 if no better than chance, to 1 for a perfect fit.

5.5 Logistic regression models selected to describe the probability of a response to motor vehicle and non motor vehicle PDAs.

The MAM of the probability of an active response to a non motor vehicle PDA per millimetre of route travelled is shown in Table 5.1. In addition to distance between the PDA and the stone curlew, response probability is dependent on the stage of breeding, PDA type, speed to fro and the presence of a dog. The MAM to describe an active response to motor vehicle PDAs per millimetre of a route travelled is also shown in Table 5.1. For this MAM, in addition to distance between the PDA and the stone curlew, response probability is dependent on speed side-to-side and whether the PDA is on a frequently used route.

5.6 Using the logistic regression models to predict the probability of a response per distance traversed of a mapped PDA event

The MAMs can be used to estimate the probability of an active response to each of the PDA events I mapped, both at sites with stone curlews and also the 34 other plots I watched where stone curlews were not present.

The methods for recording, mapping and extracting data from PDA events at sites without stone curlews were the same as for the plots with stone curlews, except that some variables did not apply (e.g. stage of breeding). Distances and speed variables were measured between the PDA and the centre of the plot instead of the location of the stone curlew. As for sites where stone curlews were present, routes of PDA events were split into millimetre sections, and for each millimetre section, the *probability of not responding per millimetre* was estimated from the models fitted in Chapter 4 (Table 5.1) using the equation:

$$\text{probability of not responding} = 1 - (e^{f(x)} / (1 + e^{f(x)}))$$

where $f(x)$ is the linear function of observed variables specified by the logistic regression models.

The product of successive values of this probability for each millimetre of the route gives an overall probability of not responding during the event. 1 minus this product gives the overall probability of a response occurring for that event. This procedure was followed for sites with and without stone curlews. Note that, at stone curlew sites the probability was calculated for every millimetre section of the PDA routes, including those observed after the focal bird had responded.

In practice, few disturbance routes come within 50m of stone curlew plots because they have been selected to be in relatively undisturbed locations. Furthermore, focal stone curlews often ran or flew before a PDA approached them within 50m. This meant that there were few millimetre sections where the PDA was less than 50m from the stone curlew or plot centre in the data sets used to obtain the MAMs to describe the probability of an active response to motor vehicle or non motor vehicle PDA events (Figure 5.2). As a result neither model could describe responses reliably below this distance. My experience in the field made me certain that a stone curlew would always run or fly if one approached very close by walking right up to the nest, whereas extrapolation of the regression models gave probabilities less than 1 at zero distance. Therefore, I presumed that at zero distance the probability of a response would always be 1 and there was an

exponential decrease in probability of a response between 0m and the model prediction at 50m.

5.7 Modelling the probability of a response to a non motor vehicle PDA

The dataset used in the MAM for non motor vehicles mostly contained walker and dog walker PDA events. However, joggers, cyclists and horse riders were included in the data set because there were insufficient numbers of these incidents to produce reliable separate MAMs. The effect of stage of breeding was not present in the MAM of active responses to jogger, cyclist and horse rider PDA events presented in Chapter 4 (Table 4.10). This suggests that the effect of stage of breeding is specific to walkers and dog walker PDA events.

Stage of breeding does not apply at sites without stone curlews so the coefficient could not be included in the calculation of probability of response at sites without stone curlews. Therefore I calculated a weighted average of the logistic regression across all breeding stages for use with walker PDA events. Using the coefficient values in Table 5.1, I calculated the intercept of the logistic regression model for each stage of breeding when the PDA was a walker (e.g. for the settlement stage the coefficient is the intercept value. For the egg stage the coefficient is the intercept value plus the parameter estimate for difference between the egg and the settlement stages). I then calculated the weighted mean intercept for walkers using the following equation:

Weighted mean intercept for walker PDA events =

$$\Sigma (\text{stage specific coefficients} * (\text{no. PDA events at each stage} / \text{total no. PDA events}))$$

The additional effect of a dog with a walker is obtained by adding the dog coefficient to the weighted mean intercept for all breeding stages. Intercept values for joggers, cyclists and horse riders were obtained by adding the specific coefficient to the intercept from Table 5.1. Again, the additional effect of a dog was calculated by adding the dog coefficient to the PDA specific intercept. The intercepts (weighted by stage for walker PDAs) for each PDA type are shown in Table 5.2 along with the other variables in the model.

The logit probability of a response in each section is then given by the parameter estimates in Table 5.2:

$$\ln(P/1-P) = \text{Intercept} - 0.008591 * \text{distance} + 0.00006135 * \text{speed to fro}$$

5.8 Modelling the probability of a response to a motor vehicle PDA

The probability of an active response to vehicle PDA events can be predicted using the coefficients in Table 5.1.

If the vehicle is on route which is regularly used by vehicles, the logit probability of a response to the PDA is calculated as follows:

$$\ln(P/1-P) = -10.7985 -0.009353 * \text{distance} -0.00005615 * \text{speed side} -2.3248$$

If the vehicle is on route which is not regularly used by vehicles, the logit probability of a response to the PDA is calculated as follows:

$$\ln(P/1-P) = -10.7985 -0.009353 * \text{distance} -0.00005615 * \text{speed side}$$

5.9 Calculation of probability of response for the whole route

The method described above produces probabilities per millimetre section of route. The accumulation of these probabilities, as described in section 5.6, gives an overall probability of an active response for the whole route (Figure 5.3).

5.10 Model performance

The accuracy of the model predictions can be assessed by comparing the actual and predicted probabilities of responses. Figure 5.4 shows the proportion of events in which an active response was observed plotted against the proportion of events the models predict an active response would be observed for bins of the shortest distance between the PDA route and the bird (which I call *closest approach distance*). This analysis is restricted to observation on plots with stone curlews. The diagram uses averages for bins of closest approach distance. The binning by distance was done separately for motor vehicle and non motor vehicle PDAs. Figure 5.4 illustrates the good the agreement between observed per event response rates and those estimated from the logistic regression analysis of per millimetre probability of responding. It also indicates the much lower per event response rate for motor vehicles than other PDA types.

Figures 5.5 and 5.6 show the ROC curves for the two minimal adequate models (including the weighted intercepts for non vehicle PDAs). The AUC value is 0.78 for non motor vehicle PDA

events and 0.89 for motor vehicles PDA events. This indicates a good fit between modelled and observed responses for both models.

5.11 Expected active response per hour at each site

These methods can be applied to all observed PDA events observed at a site to produce the expected probability of an active response for each event. Then, the sum of all event probabilities divided by the hours of observation at a site gives the *expected number of active responses per hour per site*. I calculated a settlement and season expected number of active responses per hour per site, and in subsequent chapters I use this as an alternative to disturbance event rate.

5.12 Discussion

Disturbance is usually measured as the mean frequency of potential disturbance events within a given area within a set time (e.g. Mallord, 2005, Liley, 1999, Taylor, 2002). Often different types of disturbance are combined into the index and assumed to have the same effect on the species being studied. Measuring disturbance in this way is simple and has been shown to be surprisingly effective in determining impacts of disturbance on the distribution of birds (e.g. Liley, 1999). However, this measure does not take into account the relative effects of different types of disturbance, or attributes of the disturbance including distance between the disturbance events and the focal animals. Furthermore, studies using these measures do not often consider the behavioural response of birds to the disturbance event. Similarly, behavioural studies where reaction distances are considered often do not consider the frequency of events.

The MAMs presented here and derived in Chapter 4 clearly show that the ways in which stone curlews respond to disturbance is dependent on many factors specific to the event and that these factors differ between motor vehicle PDAs and non motor vehicle PDAs. Therefore by using a mean frequency of disturbance as the measure of disturbance, the effects of some events are likely to be underestimated, whilst others will be overestimated. For example, the disturbance event rate method would assign three vehicle disturbance events per hour the same value as three dog walker events per hour even though the per event probability that the focal bird will run or fly away is much greater for dog walkers than for vehicles. Some studies (e.g. Miller *et al.*, 1998) have given weightings to PDA types in an attempt to improve disturbance data. In that study, instead of treating each incident of disturbance as one, a value of 1.5 was added to dog disturbance events, 1 was added to walker disturbance events and 0.5 was added to cyclist disturbance events. For example, if in an hour there was one walker event, three dog events and

two cyclist events, the disturbance level would not simply be 6 events per hour, it would be calculated as: disturbance level = (1+1) + (1+1.5) + (1+1.5) + (1+1.5) + (1+0.5) + (1+0.5) = 12.5. Although this method does give a higher weighting to the intuitively more disruptive event types, these weightings are arbitrary and not derived from evidence of their impact on the focal animal.

Measures of disturbance frequency have to also determine the area within which disturbance events are included. This can be either the maximum area of view for the bird, in which case details of vision and view shed need to be measured. Alternatively, events can be recorded in a fixed smaller area e.g. 100m from a nest site or 500m from a nest site. Again, this does not consider the visual acuity of the animal, and the fixed distance may exclude disturbance events that cause changes in behaviour. In addition, if zone of inclusion is too small, disturbance level may be uniformly low, and if the zone is too large, the resulting disturbance level may be uniformly high. This may not adequately represent the level of variation in disturbance across sites, as it affects the focal animal. Furthermore, the occurrence of an event at 300m is considered in the same way as an event at 100m, even though the closer event is likely to have more impact on the focal animal. It seems that, in some respects, the two approaches to measuring disturbance – behavioural responses and correlations with disturbance event rate - have been developed in isolation from each other. The aim of this chapter was to develop a method of combining information on frequency, type and spatial location of disturbance with a behavioural response to produce a single, more meaningful measure of the rate of disturbance events.

Modelling of responses using the method described in this chapter, takes into account the sensitivity of the stone curlew to the PDA events within the whole area that is thought to be visible to the bird. The models can accurately describe the per event probability of a response. It is suggested that this method of modelling behavioural response can be used to produce the probability of responding to PDA events around all potential nest sites and can replace the disturbance event rate as an explanatory variable in analyses of disturbance effects beyond behavioural responses. In a way this method provides the weighting attempted by Miller *et al* (1998) but the weighting is based on the expected behavioural response to the disturbance event, and generates an expected rate at which active responses occur which can be calculated regardless of whether the focal species is actually present.

Studies that look at the behavioural response of animals to disturbance have been criticised

because they do not usually consider the consequences of changes in behaviour at the population level (Gill *et al.*, 2001). For example, waterfowl often show a strong avoidance of humans when foraging and can react at long distances to an approaching disturbance event. However, the availability of alternative sites for feeding close by may mean that the disturbance does not influence fitness and survival in the long term. The models in this chapter on their own can not predict the consequences of disturbance beyond the behavioural response, but they do provide a more meaningful measure of disturbance with which the impacts of disturbance on settlement, distribution and breeding success can be assessed (Chapters 6 – 8).

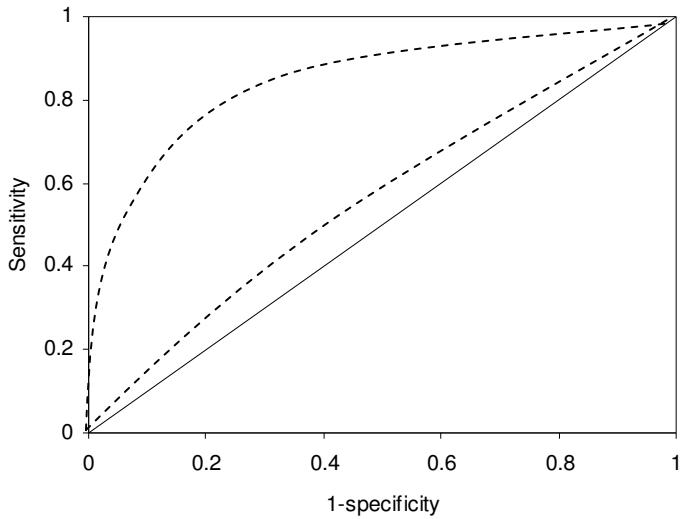


Figure 5.1. Two hypothetical ROC curves. The lower dashed line indicates a poor model performance as the line runs close to the diagonal indicating that the model is little better than chance at correctly predicting the outcome. The upper dashed line, however, shows a good model as the line occurs a larger area above the diagonal.

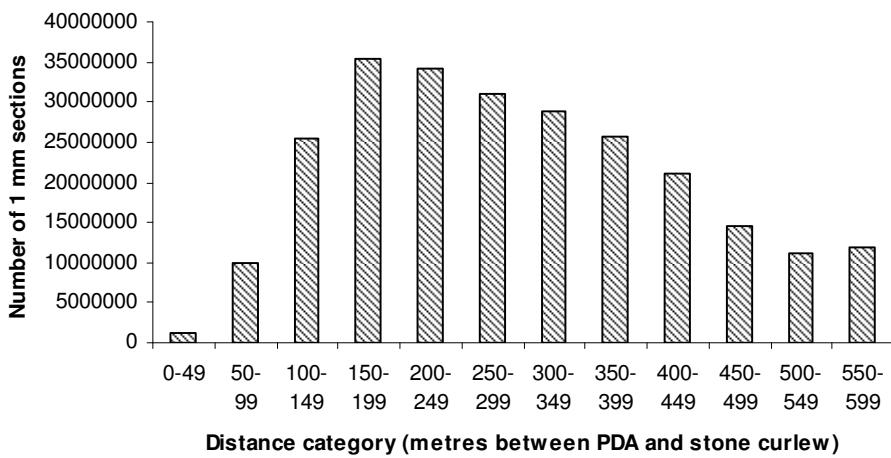


Figure 5.2. The approximate number of one millimetre sections at distances between the PDA and the stone curlew for walker PDA events.

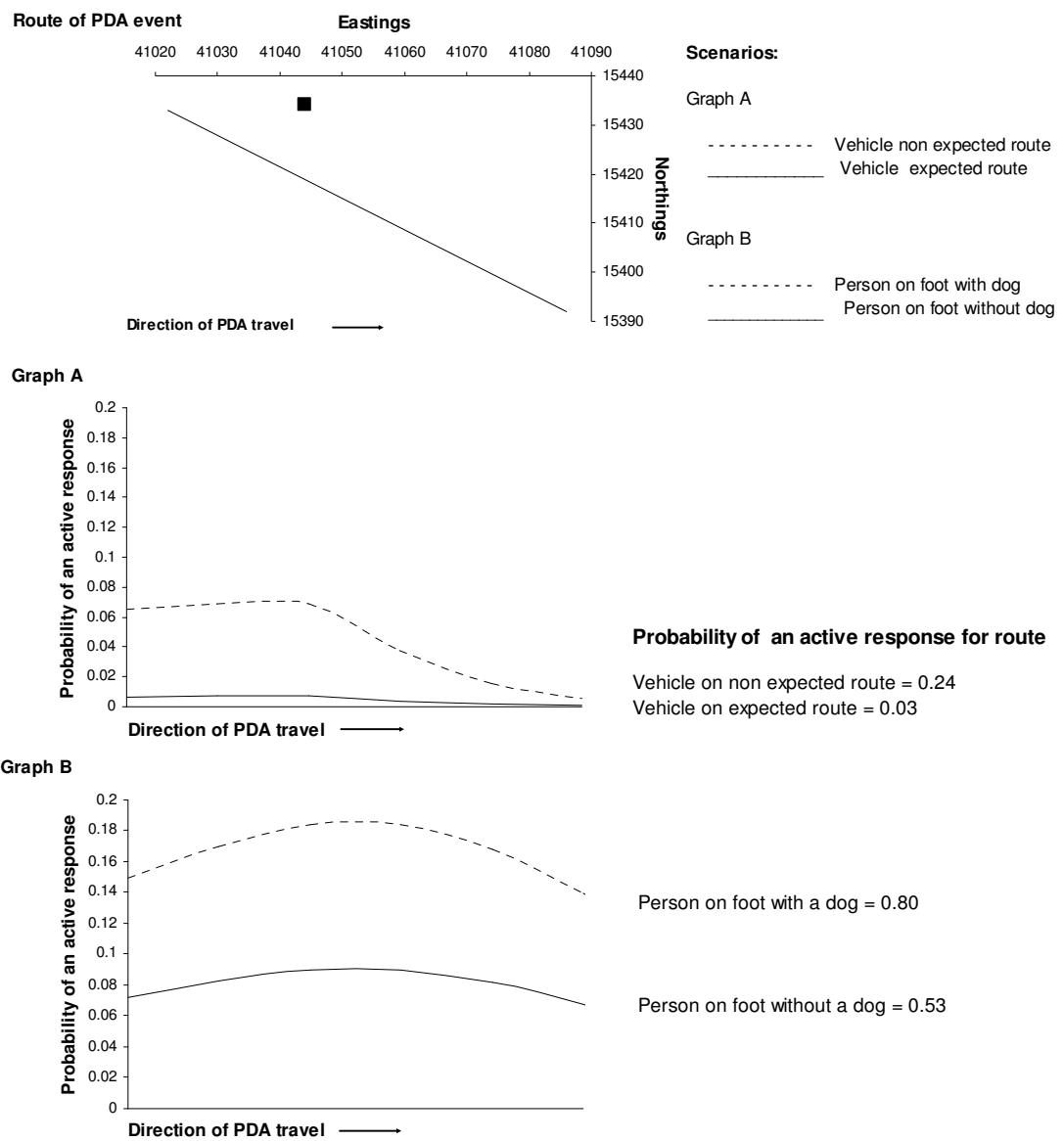


Figure 5.3. The upper part of the diagram shows a schematic map of the route taken by a PDA (line) relative to a stone curlew plot ■. Graphs A and B show the probabilities of an active response per section of route for 4 disturbance scenarios: 1) vehicle on an infrequently used route, 2) vehicle on a frequently used route, 3) person walking on foot with a dog and 4) person walking on foot without a dog. In all cases the probability of a response increase as the PDA approaches the stone curlew plot and decrease after the closest approach has been passed. The accumulation of these probabilities to give a probability of an active response being observed for the whole route, are given for each scenario. This figure is for explanatory purposes only.

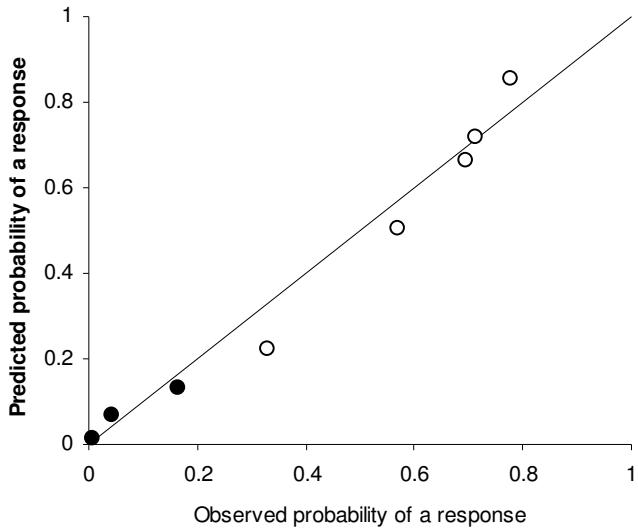


Figure 5.4. Observed probability per PDA event of an active response plotted against the predicted per event probability calculated using the MAMs. PDA events were ranked by closest approach distance and split into distance bins. Using the models to describe a response, and the known responses to each PDA event, the mean predicted and observed probabilities of a response were calculated for each bin. Closed circles are vehicle PDAs and open circles are walker PDAs. Each bin contains more than 90 PDA events. The line through 0 represents where the binned data would lie if the observed responses exactly equalled the predicted response.

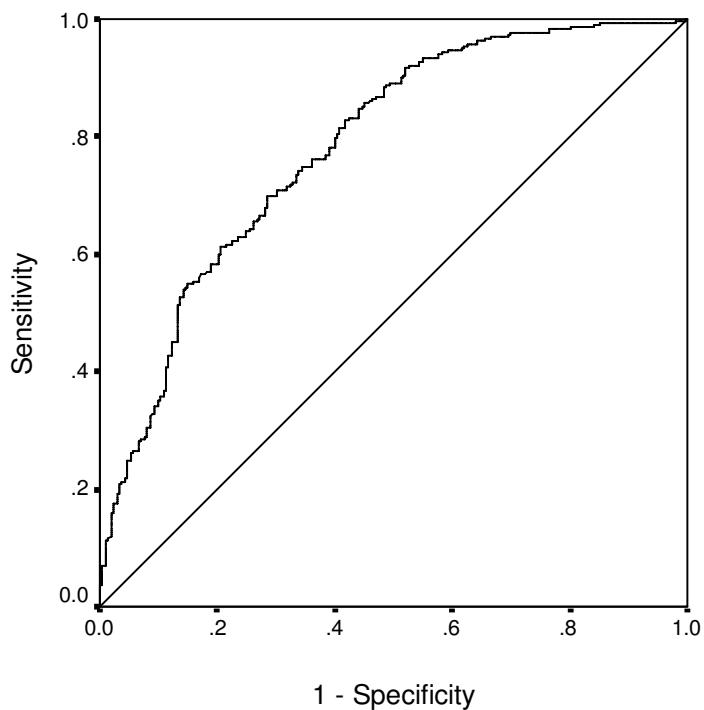


Figure 5.5. Receiver operating characteristics (ROC) curve used to assess the fit of the logistic regression models describing the probability of an active response to non motor vehicle PDA events (including the weightings by stage) (Table 2). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

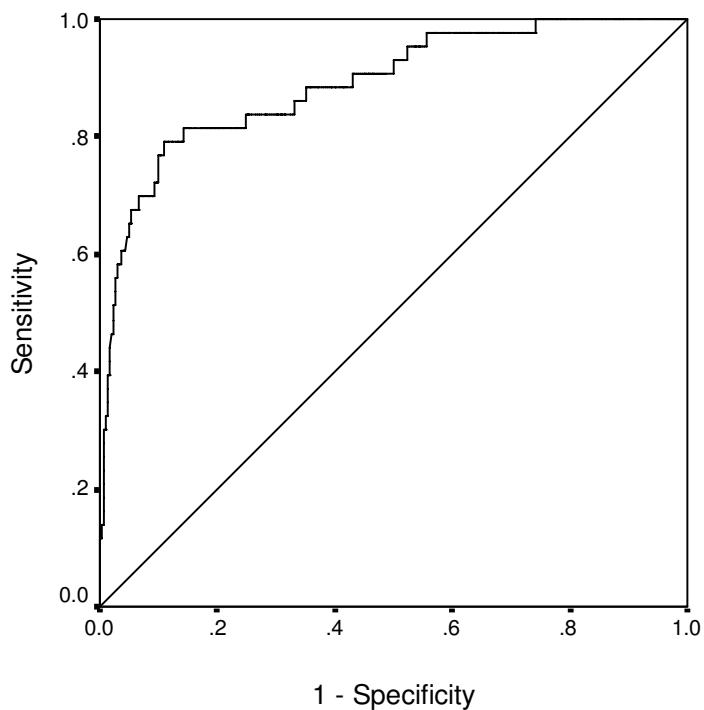


Figure 5.6. Receiver operating characteristics (ROC) curve used to assess the fit of the logistic regression models describing the probability of an active response to motor vehicle PDA events (Table 3). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

Table 5.1. Summary of the motor vehicle and non motor vehicles MAMs from Chapter 4 used to calculate the expected probability of response to PDA events at sites with and without stone curlews. The coefficients of terms in the MAM are shown.

	Non motor vehicle PDAs	Motor vehicle PDAs
Intercept	-12.2067	-10.7985
Stage:		
Settlement	0	
Egg	0.4290	
Chick	0.5196	
Post failure	-0.4706	
Roost	-0.6022	
Disturbance type:		
Walker on foot	0	
Jogger	-1.1104	
Horserider	-1.6448	
Cyclist	-2.8338	
Presence of dog	0.7674	
Speed to fro	0.00006135	
Distance from the PDA	-0.008591	-0.009353
Speed side-to-side		-0.00005615
Frequently used route		-2.3248

Table 5.2. Weighted intercepts and other parameter estimates for each non vehicle PDA type.

PDA type	Intercept	Speed to fro	Distance
Walker (and soldier)	-11.9192	0.00006135	-0.008591
Walker with dog	-11.1518	0.00006135	-0.008591
Jogger	-13.0297	0.00006135	-0.008591
Jogger with dog	-12.2622	0.00006135	-0.008591
Horse rider	-13.5641	0.00006135	-0.008591
Horse rider with dog	-12.7966	0.00006135	-0.008591
Cyclist	-14.7530	0.00006135	-0.008591
Cyclist with dog	-13.9856	0.00006135	-0.008591

6 Determining factors that affect plot occupancy by breeding stone curlews and predicting the effect of disturbance on occupancy

6.1 Summary

The selection of breeding sites by birds is thought to involve a trade-off between food availability and predation risk. Analyses of the occupancy of nesting plots by stone curlews for their first breeding attempt of the season indicate that occupancy is influenced by proximity to A roads and woodlands, the size of the breeding plot and the visibility of other breeding pairs. In addition, disturbance levels at a site during the settlement period, both in terms of disturbance event rate and the number of expected active responses per hour, have negative effects on plot occupancy.

Statistical models of plot occupancy based on disturbance measurements can be used to predict the likely impacts of changing disturbance scenarios and can guide the management of access and location of new habitat. Under current disturbance levels models predict that the removal of recreational disturbance will result in an 11% increase in plot occupancy, which is equivalent to six extra plots being occupied. The majority of this effect is due to dogs, as removal of dog walker disturbance results in a 10% increase in plot occupancy probability. It is suggested that the models presented here can be useful to those involved in managing access on stone curlew sites and to improve the siting of new plots. To aid the application of models, a software tool has been developed known as the Stone Curlew Access Response Evaluator (SCARE).

6.2 Introduction

Impacts of human disturbance on animal populations have long been studied in conservation biology (Stalmaster and Newman, 1978; Miller *et al.*, 1998; Bélanger and Bédard, 1989; Hockin *et al.*, 1992; Gill *et al.*, 2001; West *et al.*, 2002, Beale and Monaghan, 2004; Gonzalez *et al.*, 2006). A common perception is that there is a conflict between wildlife and human use of the countryside (Béchet *et al.*, 2004) and many studies address the question of how to measure the detrimental consequences of that conflict for wildlife.

Disturbance can be defined as a deviation in an animal's behaviour from patterns occurring without human influence (Frid and Dill, 2002). Gill and Sutherland (2000) identify two components to the problem of disturbance on animals. Firstly, whether disturbance causes the avoidance of areas that they would usually exploit; and secondly, whether this affects mortality,

reproductive success or population size. Most disturbance studies address the first component through either the comparison of the distribution of species at sites with differing disturbance levels (e.g. Tuite *et al.*, 1994, Sutherland and Crockford, 1993) or recording short-term behavioural response to disturbance events (e.g. Belanfer and Bedard, 1998). A small number of studies have shown impacts of human disturbance on the second component to the problem, population level effects (Liley, 1999, Beale and Monaghan, 2004, Yasue and Dearden, 2006).

In the UK, changes in statutory rights of access due to the Countryside and Rights of Way Act 2000 (CRoW) have highlighted that research on the impacts of disturbance on breeding birds is a priority. CRoW creates a right of access on foot to key habitats defined as ‘open country’: moorland, heathland, mountain, lowland grassland; as well as registered common land. Due to its conservation status, its use of ‘open country’ habitats, and the location of the only breeding populations in the United Kingdom near areas with high human population density, the stone curlew is one of the species considered to be most vulnerable to potential effects of the CRoW Act.

In response to the stone curlew population decline, the RSPB/English Nature recovery project sought to address habitat loss through the creation of alternative nesting sites. This was achieved in part through the establishment of stone curlew nesting plots, 1-2 ha areas of cultivated land within semi-natural grassland or arable crops which provide the bare, stony habitat favoured by stone curlews (Green and Griffiths 1994, Green and Taylor 1995, Green *et al.* 2000). The majority of nesting attempts by stone curlews in Wessex now occur on these specially created plots (Figure 2.3) which are permanent within the landscape. Whilst several are used regularly, others appear to be avoided or used less frequently. In Chapters 3, 4 and 5 it was shown that stone curlew behaviour is sensitive to human disturbance. It may therefore be suspected that plots with high disturbance may be avoided for breeding. In this chapter I address what variables are associated with plot occupancy for breeding by stone curlews, with particular reference to human disturbance levels around nest sites.

6.3 Aims of chapter

The aims of this chapter are to:

- 1) Determine what factors influence the use of stone curlew plots for first breeding attempts.

- 2) Produce models to describe the probability of plot occupancy for first breeding attempts in relation to measures of habitat quality and disturbance.
- 3) Test model performance in predicting plot occupancy.
- 4) Use models of plot occupancy to predict changes in plot occupancy under different disturbance scenarios

6.4 Methods

Sites were selected according to the method in section 2.4.1. Stone curlew and disturbance surveys followed the methods described in section 2.4.2 and 2.4.3. Settlement disturbance rate was calculated using the method in section 2.5.2 and the expected number of active responses per hour during settlement was calculated from models presented in Chapter 4 and methods in Chapter 5.

6.4.1 *Habitat measurements*

I measured habitat at three scales: potential nest sites e.g. stone curlew plot or habitat block; the area immediately surrounding plots or habitat blocks; and the wider landscape.

a) Nest site scale habitat assessment

There are two main types of plot in my study area: tilled plots and chalk scrape plots. Tilled plots are created by shallow (10-15 cm) cultivation of an area to remove vegetation and expose top soil and stones, creating a habitat mimicking heavily grazed, disturbed downland. When first prepared, tilled plots are completely bare because the vegetation and top soil has been turned over. Chalk scrapes are created by removing the top soil from an area with thin soil, leaving the underlying chalk exposed. This type of plot has the advantage that once prepared they do not often have to be re-managed between or within seasons as vegetation re-growth is minimal. As there is still some vegetation cover, chalk scrape plots mimic semi-natural grassland habitat to a greater extent than tilled plots. However, they can only be created where the top soil is very thin and are restricted to SPTA within my study area.

All stone curlew plots and other selected nesting sites within the study area were visited at the end of February or early March before stone curlews arrived to check they had been prepared suitably for stone curlew. I walked a diagonal transect across each plot or habitat block and took quadrat measurements, using a 1 m² quadrat split into 10-cm blocks, every 10 m. I started taking quadrat

measurements 10 m into the habitat and ended 10 m before the end of the transect. On 1-ha plots this gave approximately 12 quadrats per plot. The variables in Table 6.1 were recorded.

b) Intermediate scale habitat assessment

Habitat immediately surrounding the plot was surveyed by walking a transect parallel to one side of all plots, 10 m away from the edge of the plot into the surrounding habitat. I took quadrat measurements every 10 m, recording the variables in Table 6.1.

c) Landscape scale habitat assessment

Green *et al* (2000) reported that, although stone curlews may forage up to 3km from the nest site, most foraging activity occurs within 1 km. I therefore walked the area within 1 km radius of all plots and mapped the main habitats (1:25000 scale) and other variables in Table 6.1.

6.4.2 Deriving more meaningful habitat variables

I did not use the raw data on vegetation heights and cover as potential explanatory variables because all tilled plots that had been managed for stone curlews were completely bare during the vegetation surveys and chalk scrapes were fairly similar to one another in their vegetation cover. The main difference in vegetation between plots was associated with the type of plot: chalk scrape or tilled. Therefore this variable was included as a two level factor in analysis. I also did not use the raw intermediate scale measurements of vegetation cover and heights as variables in the analysis. Instead, I classified the habitat immediately surrounding the plot as suitable for feeding or not suitable based on the method described for landscape scale variables below and included this as a two level factor in analyses.

Instead of using all the landscape scale habitat variables as potential explanatory variables for site choice, more meaningful compound variables were derived from the data. Green and Griffiths (1994) found semi natural chalk grassland sites were used for breeding when the average sward height was less than 20 mm. Furthermore, areas were used for feeding if the average sward height was less than 50 mm (Green *et al.*, 2000). Using the data collected at the landscape scale I calculated the area suitable for breeding and the area suitable for feeding based on these values. Suitable breeding habitat included all other stone curlew plots that had been managed at the beginning of the season, semi-natural chalk grassland less than 20 mm tall, and spring sown crops less than 20 mm tall. It excluded areas of pasture and autumn-sown crops even if they were less than 20 mm tall because although stone curlews have been known to occasionally nest in these

habitats, cover of vegetation was likely to be too high for breeding by the end of March (Green *et al.*, 2000). Suitable feeding habitat included all habitats with vegetation less than 50 mm tall, including pasture and pig units but excluded winter-sown cereals in accordance with Green, Tyler and Bowden (2000). These two compound variables, distance to woodland edge, area of woodland within 1km radius (both of which may be associated with predators or landscape view) and the presence of manure heaps within 1km radius (used for feeding by stone curlews), were the variables tested at the landscape scale (Table 6.3).

6.4.3 Predator surveys

As a ground nesting species living in sparsely vegetated areas, stone curlews are vulnerable to nest predation. Corvids are common potential predators of nests, though recent studies with cameras and temperature loggers indicate that foxes may be more important as predators of stone curlew eggs and chicks (E. C. Taylor and R. E. Green, pers. obs.). An index of corvid predator abundance at a plot was measured by recording the maximum number of crows *Corvus corone*, rooks *Corvus frugilegus*, magpies *Pica pica*, jackdaws *Corvus monedula* and jays *Garrulus glandarius* seen at any one time during each 1-hour watch. The average of these maximum counts was used as the corvid index.

I did attempt to measure fox abundance in the study area, but this was abandoned, as the open landscape and lack of paths and tracks meant foxes did not use linear features to the same extent as in other studies (Mallord, 2005, Taylor, 2002), making scat counts or hair traps difficult.

6.4.4 Rabbit surveys

On semi-natural grassland stone curlews are associated with rabbits *Oryctolagus cuniculus* because rabbit grazing maintains short vegetation and disturbs soil, leaving small stones at the surface, creating suitable nesting habitat. Annual fluctuations in the density of stone curlew pairs on semi natural grassland and stone curlew nest success are positively correlated with rabbit abundance (Bealey *et al.*, 1999). This effect may be because predators may only seek out eggs and chicks when rabbits are scarce.

As rabbit abundance may be an important factor affecting plot use or nest success on a plot, rabbits were surveyed during each 1-hour watch by recording the maximum number of rabbits seen using the plot at any one time. The mean of these maximum counts was used as an index of relative rabbit abundance

6.4.5 Other landscape scale measurements

In addition I measured the variables in Table 6.2 for all plots and suitable habitat.

6.4.6 Other data

The age of the plot (years since created in the landscape) was obtained for all plots from records held by the RSPB project manager. Additionally, using past breeding records, the use of each plot by stone curlews for nesting was measured as a proportion of the years for which the plot was available in which it was used for nesting, since 1999.

6.5 Data Analysis

I used logistic regression to model the probability of a plot being occupied for breeding by stone curlews in relationship to its attributes (Table 6.3). Whether the plot was used for nesting or not was taken to be a binary dependent variable. A logit-link function and binomial error were used and linear models fitted. Models were selected by backwards stepwise elimination in which the least significant variable was removed at each stage until a Minimal Adequate Model was found (Crawley, 2002). Significance was assessed using deletion likelihood-ratio tests and comparing change in residual deviance using chi-square. The performance of the MAMs in successfully classifying occupied and unoccupied plots based on the explanatory variables was assessed using receiver operating characteristic (ROC) curves (Osborne *et al.*, 2001), as described in Chapter 5.

For this analysis I only considered the use of the artificially-created stone curlew *nesting plots*, not the areas of disturbed ground or other suitable nesting sites within the study area used in some other parts of the study. This was to standardise between nesting habitats in terms of vegetation cover, area and other characteristics. Additionally, plots were only included in the analysis if they were available for breeding stone curlews by 1 March in each year. Of the 75 plots in my study site, 56 had been managed or were suitable for nesting stone curlews by 1 March 2004 and 61 had been managed by 1 March 2005. The remaining 19 and 14 in each year respectively had not been cultivated for stone curlews since the previous summer and so retained large amounts of vegetation, making them unsuitable for breeding. The majority of these plots were managed by the end of March in each year and so did provide breeding habitat for stone curlews later, however, I excluded these from the analysis of plot occupancy because they were not available for early returning birds. Also, only plots that were created before the focal year were included. The reasoning for this is that pairs could have theoretically ‘discovered’ the plot the previous

season whereas plots new in the focal year may be avoided because they are simply unknown to stone curlews. Furthermore, I only considered first breeding attempts by each pair.

Two measures of disturbance were used in these analyses:

1. The expected number of active responses per hour during the settlement period in each year (using models from Chapter 4 and methods from Chapter 5).
2. Settlement disturbance event rate each year (Section 2.5.1).

Multiple logistic regression models relating occupancy to one of these disturbance variables and the other variables described earlier (Table 6.3) were fitted separately for 2004 and 2005. I also fitted multiple logistic regression models to pooled data for both years with these variables and year as a factor. I simplified these models by backward elimination to select MAMs. The use of data for some sites in both years in the same analysis could be regarded as pseudo-replication, but this was disregarded.

6.6 Results

6.6.1 *Models describing the probability of plot occupancy for first breeding attempts in 2004*

For both disturbance variables, the minimal adequate model of the probability of plot occupancy for a first breeding attempt in 2004 included two variables: the disturbance variable for the settlement period and whether the plot was visible from of another occupied stone curlew breeding site (Table 6.4 and 6.5). Stone curlews were significantly more likely to occupy less disturbed plots and those where there were no other pairs visible.

6.6.2 *Models describing the probability of plot occupancy for first breeding attempts in 2005*

Using the expected number of active responses per hour during settlement as a disturbance variable, the minimal adequate model of the probability of plot occupancy for a first breeding attempt in 2005 included the disturbance variable, the distance to the nearest woodland edge and the distance to the nearest A classified road (Table 6.6). Stone curlews were significantly more likely to occupy less disturbed plots, further from woodland edges and further from A roads.

Using the number settlement disturbance event rate as the disturbance variable, the minimal adequate model of the probability of plot occupancy for a first breeding attempt in 2005 included the disturbance variable, the distance to the nearest woodland edge, the distance to the nearest A

classified road, the area of the plot and the length of A classified road within a 1km radius (Table 6.7). Stone curlews were significantly more likely to occupy larger and less disturbed plots, further from woodland edges and further from A roads. Those with a higher length of A road within 1km radius were also more likely to be occupied.

6.6.3 Models describing the probability of plot occupancy for first breeding attempts in 2004 and 2005 combined

Using the expected number of active responses per hour during settlement as the disturbance variable, the minimal adequate model of the probability of plot occupancy for a first breeding attempt in both years included the disturbance variable, the distance to the nearest woodland edge and the distance to the nearest A classified road (Table 6.8). Stone curlews were significantly more likely to occupy less disturbed plots, further from woodland edges and further from A roads.

Using the settlement disturbance event rate as a disturbance variable, the minimal adequate model of the probability of plot occupancy for a first breeding attempt in both years included the disturbance variable, the area of the plot, the distance to the nearest A classified road and whether the plot was visible from another occupied stone curlew breeding site (Table 6.9). Stone curlews were significantly more likely to occupy larger, less disturbed plots, away from other breeding pairs and further from A roads.

6.6.4 Models describing the probability of plot occupancy using disturbance measures only

When examined one at a time, both disturbance variables were significant in explaining the variation in plot occupancy in both years and for the years combined (Table 6.10). Figure 6.1 shows the combined years model for both disturbance measures.

6.7 Model Performance

Figures 6.2 to 6.13 show the ROC curves for the minimal adequate models (Tables 6.4 to 10). The AUC values, standard errors and p values for each ROC curve are shown in Table 6.11.

The only model which failed to perform adequately was the 2004 MAM including settlement disturbance event rate only (Figure 6.5). The model which performed best was the 2005 MAM including settlement disturbance event rate, the distance to the nearest woodland edge, the area of the plot, the length of A road within 1km radius and the distance to the nearest A road. This good performance is expected because this MAM contains the most number of explanatory variables. It

is only meaningful to compare between models with the same type and number of explanatory variables in the MAM. Therefore only the models containing single disturbance measures should be compared. In 2004, 2005 and for the study years combined, the MAMs with the expected number of active responses per hour performed as better predictors of plot occupancy (Figures 6.4, 6.8. and 6.10) than those containing just disturbance event rate.

6.8 Predicting changes in plot occupancy with future disturbance scenarios

An important application of disturbance research is the assessment of effects of projected changes in disturbance. With the CRoW Act and changes in military training, disturbance close to stone curlew plots may increase and change in its composition of PDA types. It is important to be able to predict how these changes may effect the occupancy of stone curlew nesting sites. By using the plot occupancy models, plausible future scenarios can be investigated and the likely effect on plot occupancy determined.

6.8.1 Scenarios of change in disturbance

Although the models which contained other explanatory variables explained more of the variation in plot occupancy than those just containing disturbance measures, to predict changes under different disturbance scenarios I used the model with just the expected number of active responses per hour during settlement for both years combined (Table 6.10). The reason for this is that, if these models are used by land managers to predict changes in plot occupancy it is unlikely that the necessary additional variables will have been measured at a plot.

I simulated the following scenarios of future changes in disturbance at the plots in my study area over two years:

1. All sites:

- Current disturbance regime doubled
- 50% increase in disturbance regime
- Exclusion of dog walkers
- Exclusion of dogs (dog walkers become just walkers)
- No recreational disturbance
- No vehicle disturbance (all types)

2. Scenarios specific to SPTA:

- No military disturbance
- No civilian vehicle disturbance

- No military vehicle disturbance
- No soldiers on foot

In all cases (Figures 6.14 to 6.23) the current probability of plot occupancy for measured disturbance in 2004 and 2005 is plotted against the predicted probability of plot occupancy with a change in disturbance described by the scenario.

With a 100% or 50% increase in the current disturbance level at each site the plot occupancy model predicts that there would be a 9% and 5% reduction in the proportion of plots occupied respectively (Figures 6.14 and 6.15). This is equivalent to six and three additional breeding plots being unoccupied for breeding over the two study years.

By excluding dogwalkers on all sites (Figure 6.16) but keeping the other rates of PDAs the same, the model predicts that there would be a 10% increase in plot use, the equivalent to six extra plots being occupied. By removing dogs but presuming those walkers would still use the site without their dogs, the model predicts a 4% increase in plot use or three extra plots used (Figure 6.17). The biggest change in plot use is by excluding all recreational disturbance (Figure 6.18). Under this scenario plot use would increase by 11% and seven extra plots would be used. However, given the only slight difference between this scenario and the exclusion of dog walkers, it is clear that the main effect is through the removal of dogs.

As expected by the small behavioural response to vehicles, removal of all vehicles from sites in the study area only increases plot occupancy probability by 2% or one extra plot (Figure 6.19). By excluding all current military disturbance on SPTA but leaving recreational disturbance at current levels, there would also only be a 2% increase in plot occupancy (Figure 6.20). By excluding just military vehicles (Figure 6.22) and allowing current recreational disturbance levels, there would be an increase in plot use of 1% or less than one extra plot occupied. By excluding civilian vehicles on SPTA (Figure 6.21) but keeping military training and other recreational activities, plot occupancy would increase by 2%. Finally, by excluding soldiers on foot on SPTA the probability of plot occupancy would rise by only 0.2% (Figure 6.23).

6.9 Discussion

When choosing nests sites, individual birds are expected to maximise their survival and reproductive success (Morris, 1987, Orians and Wittenberger, 1991, Valkama *et al.*, 1998).

However, sites may rank differently in their quality according to food resources and safety from predators of the adults and chicks. Therefore, site choice usually reflect compromises between sufficient resources to meet different requirements, for example, food availability, suitability of nest sites and low predation risk (Valkama *et al.*, 1998). It is thought that birds respond to a perceived risk of disturbance in the same way they respond to the risk of predation (Frid and Dill, 2002). Therefore, since several studies suggest that breeding territories associated with a high risk of predation should be avoided by birds (Newton, 1998, Roos and Part, 2004), it is probable that disturbed areas are also avoided by breeding birds because the perceived risk of predation of eggs, chicks or themselves is higher.

It has been shown in this chapter that several variables influence plot occupancy for first breeding attempts by stone curlews and the variables that were common to all models and had a very strong effect, were the two measures of disturbance during the settlement period. Both the settlement disturbance event rate and the expected number of active responses per hour during settlement (from the models presented in Chapter 4) had a significant effect on whether the plot was used for a first breeding attempt. When disturbance event rate only was considered, the model predicted a 62% probability of occupancy if there was no disturbance. At one disturbance event per hour there is a 29% reduction in the probability of plot occupancy, at two events per hour the reduction is 55%, at three events per hour the reduction is 74%, and at four events per hour the reduction is 86%. The plot occupancy model based on expected rate of active responses predicts that at zero expected active responses per hour there is a 62% chance of a plot being occupied. If the stone curlew is expected to show one active response per hour there is a 71% reduction in the probability of plot occupancy, at two active responses per hour the reduction is 96% and at three active responses per hour the reduction is 99%.

There is a great deal of literature on the effects of human disturbance on the distribution and use of habitat by birds (e.g. Finney *et al.*, 2004, Yalden, 1992, Green *et al.*, 2000, Schultz and Stock, 1993, Burger 1986, 1991, 1994, Burger *et. al.* 1995, Strauss and Dane 1989, Lafferty, 2001, McCrary and Pierson, 2000, Madsen, 1985). Results from such studies are variable in the effects of disturbance shown and there are usually also strong effects of habitat quality and other factors which may obscure effects of disturbance. For example, Finney *et al.* (2003) demonstrated that recreational disturbance on moorland had a significant effect on the distribution of golden plovers *Pluvialis apricaria* during the breeding season. Specifically, golden plovers tended to avoid areas within 200 m of a heavily used long distance footpath during the chick-rearing period. Visitor

pressure on this footpath, however, was high (60+ visitors per day) and on a site with approximately half this visitor pressure the effect of footpath avoidance was not observed. Conversely, in a study of dunlin *Calidris alpina* at the same sites, the authors report a significant negative relationship between the probability of a grid square being occupied for breeding and distance to the footpath. However, it was thought probable that the birds were responding to some underlying environmental variation, such as the distribution of peat pools, which was not measured in the study.

The importance of measuring additional aspects of nest site selection is demonstrated by a study of common sandpipers *Actitis hypoleucus* breeding around an upland reservoir in the Peak District National Park. Yalden (1992) reports that pairs of sandpipers set up territories and subsequently bred in areas where there were fewer visitors and anglers. However, these areas also differed in terms of habitat which was not measured in the study, so whilst there was a correlation between site use and disturbance it was not clear what was the major driver of habitat selection. In a study of the cinereous vulture *Aegypius monachus* for example, nest site choice was found to be influenced by isolation from human disturbance but this variable was not independent of slope or climatic variables (Moran-Lopez *et al.*, 2006).

The effect of human disturbance on the distribution of birds outside the breeding season has also been widely studied and results are equally variable and thought to be associated with other factors. Madsen (1985) reports a reduction in geese utilisation of fields for feeding in autumn if disturbance exceeds a threshold. In particular and similarly to my study of stone curlews, disturbance events that caused geese to take flight were identified as being major factors in the decline in field use, but additional important factors determining field use were the presence of woodlands and barriers that may hide predators. Lafferty (2001) observed no clear effects of recreational disturbance on the distribution of shorebirds on beaches in winter feeding flocks, instead suggesting that habitat features play a more important role in determining the usage of areas. The result is consistent with McCrary and Pierson (2000) who did not see an effect of human activity on shorebird habitat use. However, in both of these studies, the area of measurement was restricted to only one site and the distribution of birds was measured within a small area. When multiple sites were considered a negative association between the distribution and abundance of shorebirds using sites and disturbance was observed (McCrary and Pierson, 2000). Burger (1986) additionally saw a negative effect of disturbance on bird distribution when comparing between sites at large spatial scales.

Effects of human disturbance on distribution have also been shown to not be restricted to birds. Yalden (1990b) reports that the distributions of red deer *Cervus elaphus* and red-necked wallabies *Macropus rufogriseus* in the Peak District, England, are affected by the distribution of recreational activities through the park. Both species associated with areas of low disturbance and abandoned the use of formerly undisturbed areas when they become open to the public. In another mammalian study, Fairbanks and Tullous (2002) recorded the distribution of pronghorn *Antilocapra americana* before a park was opened for public recreation and in the three years after and showed that pronghorn occurred significantly further from sources of human disturbance and tracks in the years where disturbance was higher. Analysis of 70 potential breeding sites by Southern fur seals *Arctocephalus australis* showed that sites which were used for breeding were likely to be less disturbed and in areas where perceived predation risk is lower (Stevens and Boness, 2003).

When only disturbance variables were considered, the models presented in this chapter can only predict a 62% probability of plot occupancy by stone curlews where there is no disturbance. This suggests that occupancy is also affected by other factors. As mentioned for other studies, additional factors are usually important in determining nest site choice or habitat use and much of the remaining variability in stone curlew plot occupancy is explained by additional variables in the full models. Plots close to roads had a lower probability of occupancy than those further away. In an analysis of 14 years of stone curlew data, Day (2003) showed that stone curlews avoided nesting close to main trunk routes and A classified roads, with densities lowered up to 3500 m from the busiest roads. Green *et al.* (2000) also showed this effect within one breeding year in Wessex and Breckland. The mechanism for road avoidance may be noise or lights from headlights. Day (2003) considered the major mechanism to be the latter as this may interfere with foraging ability at night.

Plots where other breeding pairs were visible were less likely to be occupied in 2004. At first this seems an unlikely result as on semi-natural habitat, such as rabbit grazed downland on Porton Down, several pairs of stone curlew occupy the same continuous habitat ‘patch’ and appear to tolerate each other’s presence. Stone curlew pairs have been observed to nest at distances less than 100m from each other (E.C. Taylor pers obs. and P. Sheldrake pers. comm.) in this sort of habitat. However, examination of such sites usually shows that where stone curlews nest close to one another they are actually hidden from each other’s view by vegetation or topography. Until

2006, there had never been an incident of more than one pair occupying the same specially created stone curlew plot. This suggests that although stone curlews will tolerate other nesting pairs nearby, they are less tolerant of other pairs within sight. In addition, the *actual distance to the next occupied plot* was included as an explanatory variable in the modelling but was not significant in any of the models, further supporting the idea that stone curlews may nest close (as is the case on semi-natural sites) but it is the *visibility* of other pairs that is important.

Plots close to woodland edges were avoided by stone curlews in 2005, possibly because they are viewed as having high predation risk (Stroud *et al.*, 1990, Warren, 2000). Woodland provides refuge for badgers and foxes, both important nest and chick predators (Wallender *et al.*, 2006). Furthermore, corvid predators use woods for nesting and the edges as perches from which to feed (Wallender *et al.*, 2006). Yasue (2006) observed that feeding shorebirds selected beaches further from forest edges because of perceived predation risk being higher and it was thought that this was the main habitat selection variable rather than food availability or human disturbance. In a study of golden plover habitat use in the Peak District, Finney *et al.* (2003) showed that golden plovers avoided grid squares in close proximity to a forest plantation, again probably because perceived predation risk was higher there.

Woodland also creates barriers to fields of view and as stone curlews have a preference for open downland, blocks of woodland close to plots may create less favourable habitat. This mechanism has been suggested for the variation in the spatial distribution of nests for other waders (Koivula and Ronka, 1998, Amat and Masero, 2004, Wallender *et al.*, 2006, Berg *et al.*, 1992, Galbraith, 1988, Gotmark *et al.*, 1995). Breeding close to features that break up the landscape view may mean perceived predation risk is higher as stone curlews may not be able to detect predators at long distances and have enough time to react. It has been suggested that golden plovers preferentially select areas where their field of view is optimal, allowing them to detect predators at a greater distance (Ratcliffe, 1976; Whittingham, *et al.*, 2002, Finney *et al.*, 2003).

In some models the area of the plot was a contributing factor in nest site choice, with larger plots being preferred over smaller ones. Moran-Lopez (2006) also found that larger habitat patches increased the likelihood of a site being used for breeding by cinereous vultures. It is thought that predators allocate increased hunting effort where prey is most vulnerable (Newton, 1998, Quinn and Cresswell, 2004). Stone curlews nesting on plots may be already considered vulnerable to predators because plots are small, strikingly different to the surrounding habitat and obvious in

the landscape and as a result predators may learn to look for them and then search within them for nests and chicks. Therefore, smaller plots may be even more vulnerable to predation because there is a smaller area to search for nests. Food availability on plots were not measured in this study but smaller plots may have less invertebrate food for stone curlews and so larger plots may be selected.

Other habitat variables were not important factors in any models. Stone curlews were no more likely to occupy plots where there was a larger area of suitable feeding habitat close by, if the habitat immediately off the plot was suitable for feeding, or if the plot was situated in grassland or arable habitat. Furthermore, plot type (tilled or chalk scrape), slope and aspect were not significant factors. In a study of SPTA plots, Green, Ash and Austin (unpublished) reported that chalk scrape plots were significantly more likely to be occupied over tilled plots, possibly because chalk scrapes resemble semi-natural chalk grassland to a greater extent. However, this was confounded by the effect of roads in determining plot use, as chalk scrape plots are further from main roads. Lack of significance of habitat variables in determining plot use is likely to be a product of plot placement in the landscape. When plots are created there is thought as to the suitability of the position in the landscape with respect to factors such as feeding habitat nearby and distance to main roads. One of the easiest aspects of suitability to measure is feeding habitat (P. Sheldrake pers. comm.) and effort is made to provide stone curlews with access to feeding sites. As a result, and because I was working within the core of the population centred around Salisbury Plain, all plots in my study area have large areas of suitable feeding area within a 1 km radius.

Other variables that may act as surrogates for disturbance were not significant in any models, despite their importance in other studies of habitat occupancy (e.g. Moran-Lopez *et al.*, 2006, Fargallo *et al.*, 1998, Atienza *et al.*, 2001; Cramp and Simmons, 1980). In a similar comparative study of used and unused nest sites, Gavashelishvili and McGrady (2006) found that nest site occupancy by bearded vultures *Gypaetus barbatus* was partly determined by distance to roads. However, the number of humans living within a 20 km radius and the distance to the nearest populated area were not important. In the same study, Eurasian griffon vultures *Gyps fulvus* were not affected by any of the measured human disturbance surrogates. Moran-Lopez *et al.* (2006) stress that the use of variables such as distance to village etc is not that useful because it is the accessibility of areas that can influence the use more than the population of humans around a site. All areas may be considered equally accessible if they are near roads as people are as likely to get

in their cars and go somewhere as they are to walk from their homes. Given that disturbance surrogates were not correlated with disturbance rates in Chapter 2, these results are perhaps not surprising.

Whilst many studies appear to suggest there is an effect of disturbance on habitat use, it is important to establish if effects are long term and result in reduced use of habitat over a longer period, or if effects are simply short-term changes in spatial distribution that will be reversed later (Gill, Sutherland and Watkinson, 1996). For example, Pfister *et al.*, (1992) report that four of seven shorebird species at a beach staging area in east coast America showed movement in response to disturbance either by shifting roost site or leaving the area completely. However, those that could compensate for reduced habitat quality as a result of disturbance and moved areas did not show a long term population decline because there were alternative habitats to use. In a second study, where disturbance levels on inland lakes in England exceeded the tolerance threshold of many waterbirds, sites were abandoned but this disturbance did not have any long-term effects on the population (Tuite *et al.*, 1984). In fact, at the same time species were decreasing their use of disturbed water bodies, populations of most species increased dramatically. The reasoning was that the increase in recreational activity occurred during a time of increased habitat creation through the building of many new reservoirs enabling birds to adapt and redistribute to non disturbed sites.

At present stone curlews are not habitat limited in Wessex and they may be able to compensate for sites that are unsuitable in terms of disturbance by nesting on an alternative plot. As the population continues to grow, however, competition for plots is likely to increase and stone curlews will have to choose to either compete for undisturbed plots, move further out of the core of the population to find suitable breeding plots, use the disturbed plots, or not breed at all. All of these options may have consequences for stone curlews at the population level. A small number of studies have linked effects of disturbance to population level consequences (Beale and Managhan 2004, Finney, Pearce-Higgins and Yalden 2005, Liley, 1999). For example, Liley (1999) showed that territory use and consequent productivity of ringed plovers *Charadrius hiaticula* was markedly affected by human disturbance, resulting in significant reductions in population size at least at a local scale.

Whilst the best long term option for stone curlew conservation may be to provide semi natural

habitat with minimal management, such as downland, changes in grazing and the modern farming system mean that this will probably never be possible on a large scale. Therefore, stone curlew plots provide a relatively easy way of supporting a vulnerable species, but as their creation and management is expensive, their potential performance should be maximised through increased consideration of placement in the landscape. In particular, this study has shown that aspects to do with human disturbance should be taken into account.

The scenarios presented in this chapter clearly show that the probability of plot occupancy can be maximised by the exclusion of recreational disturbance and in particular that involving dogs. Across both years the models predict that there would be a 9-11% increase in the probability of plot occupancy, which translates to 5-6 extra plots likely to be occupied each year. Exclusion of disturbance by the military and vehicles did not show a large increase in plot occupancy probability. By excluding disturbance by these PDA events on sites in the study area the model predicts that only an additional 1-3 plots may be used. This is expected given that the probability of a stone curlew responding to a vehicle PDA event is much lower than for a person on foot. This highlights the importance of being able to distinguish between the types of disturbance that result in significantly reduced plot use from those that do not, in the management of recreational access and military training, and the creation of new habitat. However, it should be noted that the scenarios are exclusions based on *current* rates of expected active responses and mostly do not predict the change from increasing disturbance.

However, total exclusion of disturbance around stone curlew sites is costly, time consuming and probably unnecessary. A solution used in many areas is the management of access through buffer zones or set-back distances where disturbance is excluded within a certain distance, usually based on flush distances (Rodgers & Schwikert 2002, Richardson & Miller 1997, Rodgers & Smith 1995). However, as discussed in previous chapters, buffer zones based purely on a behavioural response are inadequate. It is therefore suggested that, for stone curlew sites, the behavioural models described in Chapter 4 and 5 and plot occupancy models described in this chapter, can provide practical value to users interested in the impact of specified patterns of disturbance. Firstly, behaviour models and the method in Chapter 5 can quantify the per event probability of a stone curlew responding in a particular way to a hypothetical PDA event with specified characteristics. Secondly, this can be translated in the probability of plot occupancy using models in this chapter.

To aid the evaluation of the impact of specified disturbance at real sites, the statistical models have been used to construct a software package known as the Stone Curlew Access Response Evaluator (SCARE) in collaboration with Rhys Green (RSPB) and James Perrins (exeGesIS Spatial Data Management Ltd). SCARE is a user-friendly interface whereby the user can take a built-in map, digital terrain model and information on screening vegetation for a real site and explore the consequences of various patterns of access to that site (e.g. different disturbance types and frequencies, path or track routes) and various mitigation measures (e.g. closure of areas, additional screening with boards or hedges, redirection of paths, relocation of stone curlew nesting plots). The user can specify stone curlew locations (e.g. nest sites) using real location data or proposals for the creation of artificial nesting plots. The user can also specify and alter routes likely to be used by PDAs, and PDA types and frequencies. The relationship between plot occupancy and the modelled rate of disturbance can then be used to estimate the expected reduction in the probability of the plot being used by nesting stone curlews, compared with what would be expected with no disturbance. The impact of changing the disturbance scenario can then be explored. For example, the user can change the type and frequency of PDAs, the location of an access route, the location or size of an open access or closed area, or the location of screening vegetation, and obtain revised estimates of the impact on stone curlews.

SCARE reconciles the need for public access to open landscapes with the need for continued conservation of stone curlews at existing and future potential breeding sites. It offers a way to assess the effects of hypothetical scenarios for future changes in disturbance type, routes and frequency, including the manipulation of disturbance levels. As a result it is anticipated that SCARE will be valuable in informing decisions concerning areas to be opened up for access or closed for part of the year when stone curlews are breeding. The tool is currently being used to assess changes in military disturbance on SPTA and it will be available to all those involved in stone curlew conservation in the UK.

Table 6.1. Variables measured at the nest site (N), intermediate (I) and landscape scales (L).

Scale	Variables measured	Details
N	Plot type	Tilled plot, chalk scrape plot/semi-natural habitat.
N	Aspect	Predominant direction plot faces.
N	Area of habitat block	Total area of suitable breeding habitat, ha.
N	Slope	Classified as flat or sloping based on position in landscape. Defined by eye but checked on map later and all those classed as sloped have a >5m height difference within the habitat block or plot.
NI	Percentage cover of vegetation	Estimated by eye into 10% cover classes.
NI	Percentage bare ground	Estimated by eye into 10% cover classes.
NI	Percentage cover of stones <2cm	Stones <2cm are often used by stone curlews in nests. Estimated by eye into 10% cover classes.
NI	5 measurements of vegetation height (from which a mean was taken)	Heights measured with a tape measure randomly within the quadrat, mm.
NI	Maximum vegetation height	Height of the highest vegetation in the quadrat, mm.
NI	Minimum vegetation height	Height of the lowest vegetation in the quadrat, mm.
I	Surrounding habitat	Habitat immediately surrounding plot. Classified as grassland or arable.
I	Crop type if arable	Identified in the field if crop was showing. Checked with landowner for prepared fields and fields with no crops showing.
L	Area of woodland	Estimated from mapping, ha.
L	Area of scrub	Estimated from mapping, ha.
L	Area of unimproved semi-natural chalk grassland and approximate height	Estimated from mapping, ha. Heights in blocks of habitat estimated by eye, mm.
L	Area of improved grassland and approximate height	Estimated from mapping, ha. Heights in blocks of habitat estimated by eye, mm.
L	Area of spring sown arable crops	Sown after 31 st December of previous year.
L	Area of winter sown arable crops	Sown before 31 st December of previous year.
L	Crop types at field level	Identified in the field if crop was showing. Checked with landowner for prepared fields and fields with no crops showing.
L	Crop height at field level	Heights in blocks of habitat estimated by eye, mm.
L	Area of pig units	Estimated from mapping, ha.
L	Manure heaps	Presence of manure heaps in 1km radius.
L	Area of set aside	Estimated from mapping, ha.
L	Area of fallow	Estimated from mapping, ha.
L	Area of sheep pasture	Estimated from mapping, ha.
L	Area of cow pasture	Estimated from mapping, ha.

Table 6.2. Other variables measured around plots and other suitable breeding habitat within the study area.

Variable	Description
Distance to A road (m)	Shortest straight line distance from the centre of the plot to the nearest A classified road
Length of A road within 1 km radius of plot (m)	The total length of A road with 1km radius
Distance to track (m)	Shortest straight line distance from the centre of the plot or habitat block to the track easily accessible by a vehicle (surrogate for access point), m
Distance to nearest village (m)	Shortest straight line distance from the centre of the habitat to the edge of nearest settlement with 20+ houses
Area of village within 1 km radius (ha)	Total area of village within 1 km radius
Distance to next occupied plot by time of arrival	Shortest straight line distance from the centre of the plot to the next nearest occupied habitat
Next occupied site in line of sight	Variable indicating if the next nearest occupied plot is within visibility to stone curlews on the focal site.
Distance to core of population	Harmonic mean distance to all known breeding attempts 2000, 2002 and 2003

Table 6.3. Variables included in the plot occupancy models.

Variable	Variable type
Expected number of active responses per hour during settlement	Continuous
Settlement disturbance event rate	Continuous
Breeding pair visible from focal plot (yes=1, no=0)	Factor, 2 levels.
Distance to nearest woodland edge (m)	Continuous
Distance to nearest A road (m)	Continuous
Distance to nearest vehicle accessible track (m)	Continuous
Distance to next occupied plot (m)	Continuous
Length of A road with 1 km radius (m)	Continuous
Distance to nearest village (m)	Continuous
Presence of village within 1 km radius (yes=1, no=0)	Factor, 2 levels
Area of village within 1 km radius (ha)	Continuous
Distance to core of population (m)	Continuous
Area of suitable feeding habitat within 1 km radius (ha)	Continuous
Surrounding habitat: grassland or arable	Factor, 2 levels,
Area immediately off plot suitable for feeding (yes=1, no=0)	Factor, 2 levels
Presence of manure heap within 1 km radius (yes=1, no=0)	Factor, 2 levels
Aspect	Factor, 4 levels
Plot type	Factor, 2 levels
Area of plot (m ²)	Continuous
Slope of plot	Factor, 2 levels
Rabbit index	Continuous
Corvid index	Continuous
Year	Factor, 2 levels.
Age of plot	Continuous
Proportion of years used by stone curlews since created	Continuous

Table 6.4. Parameter estimates from a logistic regression model relating the probability of plot occupancy for first breeding attempts in 2004 to the expected number of active response per hour during the settlement period and whether a breeding pair at another site was visible from the plot.

Variables in the MAM are shown in bold. Changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for these variables for the effect of deleting each variable from the final MAM. For variables not present in the MAM, the effect of adding each non significant variable is shown. The residual deviance of the model is 64.37 with 53 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	0.2542			
Expected number of active responses per hour during settlement	-2.5896	7.12	1	0.0075
Breeding pair visible from plot	-0.8179	5.94	1	0.014
Distance to woodland edge (m)		1.43	1	0.23
Distance to nearest A road (m)		0.36	1	0.54
Distance to next occupied plot (m)		2.21	1	0.13
Aspect		0.17	3	0.98
Length of A road with 1km radius (m)		0.93	1	0.33
Distance to core of population		0.0021	1	0.96
Area of suitable feeding habitat within 1km radius		0.030	1	0.86
Surrounding habitat		0.24	1	0.61
Area immediately off plot suitable for feeding		0.026	1	0.87
Distance to nearest village		0.45	1	0.49
Village with 1km radius		0.61	1	0.43
Area of village within 1km radius		0.054	1	0.81
Rabbits		0.51	1	0.47
Corvids		0.11	1	0.73
Area		0.71	1	0.39
Slope		1.34	1	0.24
Plot type		1.92	1	0.16
Distance to vehicle accessible track		2.52	1	0.11
Age of plot		0.42	1	0.51
Use by stone curlews since created		1.61	1	0.20
Presence of manure heaps		2.10	1	0.14

Table 6.5. Parameter estimates from a logistic regression model relating the probability of plot occupancy for first breeding attempts in 2004 to the number of disturbance events per hour during the settlement period and whether a breeding pair at another site was visible from the plot.

Variables in the MAM are shown in bold. Changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for these variables for the effect of deleting each variable from the final MAM. For variables not present in the MAM, the effect of adding each non significant variable is shown. The residual deviance of the model is 66.53 with 53 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	0.1816			
Settlement disturbance event rate	-0.7801	4.96	1	0.025
Breeding pair visible from plot	-0.8052	5.85	1	0.015
Distance to woodland edge (m)		0.21	1	0.64
Distance to nearest A road (m)		0.96	1	0.32
Distance to next occupied plot (m)		2.18	1	0.14
Aspect		0.13	3	0.98
Length of A road with 1km radius (m)		1.32	1	0.24
Distance to core of population		0.23	1	0.62
Area of suitable feeding habitat within 1km radius		0.013	1	0.90
Surrounding habitat		0.37	1	0.53
Area immediately off plot suitable for feeding		0.0010	1	0.97
Distance to nearest village		0.85	1	0.35
Village with 1km radius		0.64	1	0.42
Area of village within 1km radius		2.21	1	0.13
Rabbits		2.67	1	0.10
Corvids		2.27	1	0.13
Area		2.54	1	0.11
Slope		1.91	1	0.16
Plot type		1.42	1	0.23
Distance to vehicle accessible track		1.21	1	0.26
Age of plot		0.074	1	0.78
Use by stone curlews since created		2.15	1	0.14
Presence of manure heaps		1.56	1	0.21

Table 6.6. Parameter estimates from a logistic regression model relating the probability of plot occupancy for first breeding attempts in 2005 to the expected number of active responses per hour during the settlement period, the distance to the nearest woodland edge and the distance from the nearest A classified road.

Variables in the MAM are shown in bold. Changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for these variables for the effect of deleting each variable from the final MAM. For variables not present in the MAM, the effect of adding each non significant variable is shown. The residual deviance of the model is 71.20 with 57 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	-1.6538			
Expected number of active responses per hour during settlement	-2.3609	4.95	1	0.026
Distance to woodland edge (m)	0.002496	6.4852	1	0.010
Distance to nearest A road (m)	0.0006555	4.82	1	0.028
Breeding pair visible from plot		0.11	1	0.73
Distance to next occupied plot (m)		0.28	1	0.59
Aspect		0.96	3	0.80
Length of A road with 1km radius (m)		3.10	1	0.078
Distance to core of population		0.19	1	0.65
Area of suitable feeding habitat within 1km radius		0.19	1	0.65
Surrounding habitat		0.14	1	0.70
Area immediately off plot suitable for feeding		0.56	1	0.45
Distance to nearest village		0.70	1	0.39
Village with 1km radius		0.65	1	0.41
Area of village within 1km radius		0.85	1	0.35
Rabbits		0.0090	1	0.92
Corvids		0.025	1	0.87
Area		2.88	1	0.089
Slope		3.28	1	0.069
Plot type		1.80	1	0.17
Distance to vehicle accessible track		3.34	1	0.067
Age of plot		0.47	1	0.48
Use by stone curlews since created		1.70	1	0.19
Presence of manure heaps		0.78	1	0.37

Table 6.7. Parameter estimates from a logistic regression model relating the probability of plot occupancy for first breeding attempts in 2005 to the number of disturbance events per hour during the settlement period, the distance to the nearest woodland edge, the distance from the nearest A classified road, the area of the plot and the length of A road within 1km radius.

Variables in the MAM are shown in bold. Changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for these variables for the effect of deleting each variable from the final MAM. For variables not present in the MAM, the effect of adding each non significant variable is shown. The residual deviance of the model is 62.65 with 55 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	-4.3067			
Settlement disturbance event rate	-1.2652	6.46	1	0.011
Distance to woodland edge (m)	0.002710	6.74	1	0.0094
Distance to nearest A road (m)	0.001465	10.12	1	0.0014
Area (m²)	0.00004580	4.25	1	0.039
Length of A road with 1km radius (m)	0.0004423	4.02	1	0.044
Breeding pair visible from plot		1.31	1	0.25
Distance to next occupied plot (m)		0.75	1	0.38
Aspect		2.93	3	0.40
Distance to core of population		0.41	1	0.51
Area of suitable feeding habitat within 1km radius		0.050	1	0.82
Surrounding habitat		0.37	1	0.53
Area immediately off plot suitable for feeding		0.35	1	0.55
Distance to nearest village		0.85	1	0.35
Village with 1km radius		0.37	1	0.53
Area of village within 1km radius		0.45	1	0.49
Rabbits		0.31	1	0.57
Corvids		0.000065	1	0.97
Slope		0.90	1	0.16
Plot type		4.00	1	0.052
Distance to vehicle accessible track		3.38	1	0.065
Age of plot		0.064	1	0.79
Use by stone curlews since created		0.59	1	0.44
Presence of manure heaps		1.56	1	0.21

Table 6.8. Parameter estimates from a logistic regression model relating the probability of plot occupancy for first breeding attempts in 2004 and 2005 to the expected number of active response per hour during the settlement period, the distance to the nearest woodland edge (m) and the distance to the nearest A classified road (m).

Variables in the MAM are shown in bold. Changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for these variables for the effect of deleting each variable from the final MAM. For variables not present in the MAM, the effect of adding each non significant variable is shown. The residual deviance of the model is 144.48 with 113 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	-0.8782			
Expected number of active responses per hour during settlement	-2.1921	9.91	1	0.0016
Distance to woodland edge (m)	0.001632	5.83	1	0.015
Distance to nearest A road (m)	0.0004152	4.086	1	0.043
Breeding pair visible from plot		3.38	1	0.065
Distance to next occupied plot (m)		3.044	1	0.081
Aspect		0.73	3	0.86
Length of A road with 1km radius (m)		0.18	1	0.66
Distance to core of population		0.31	1	0.57
Area of suitable feeding habitat within 1km		0.23	1	0.62
Surrounding habitat		0.11	1	0.73
Area immediately off plot suitable for feeding		0.00023	1	0.98
Distance to nearest village		1.62	1	0.20
Village with 1km radius		0.00064	1	0.97
Area of village within 1km radius		0.036	1	0.84
Rabbits		0.24	1	0.62
Corvids		0.34	1	0.55
Area		1.99	1	0.15
Year		0.097	1	0.75
Slope		0.71	1	0.39
Plot type		3.73	1	0.053
Distance to vehicle accessible track		1.054	1	0.30
Age of plot		0.036	1	0.84
Use by stone curlews since created		1.60	1	0.20
Presence of manure heaps		1.89	1	0.16

Table 6.9. Parameter estimates from a logistic regression model relating the probability of plot occupancy for first breeding attempts in 2004 and 2005 to the number of disturbance events per hour during the settlement period within 300m radius of the plot, the area of the plot (m^2), the distance to the nearest A classified road (m) and whether a breeding pair is visible from the plot (factor).

Variables in the MAM are shown in bold. Changes in deviance, degrees of freedom and *p*-values from a likelihood-ratio test are shown for these variables for the effect of deleting each variable from the final MAM. For variables not present in the MAM, the effect of adding each non significant variable is shown. The residual deviance of the model is 139.18 with 112 degrees of freedom.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	-1.1969			
Settlement disturbance event rate	-0.9680	12.26	1	0.00046
Area of plot (m^2)	0.00003774	6.49	1	0.010
Distance to nearest A road (m)	0.0004395	4.57	1	0.032
Breeding pair visible from plot	-0.6124	6.07	1	0.013
Distance to woodland edge (m)		2.63	1	0.10
Distance to next occupied plot (m)		0.93	1	0.33
Aspect		0.57	3	0.90
Length of A road with 1km radius (m)		0.066	1	0.79
Distance to core of population		0.87	1	0.34
Area of suitable feeding habitat within 1km		0.086	1	0.76
Surrounding habitat		0.0057	1	0.93
Area immediately off plot suitable for feeding		0.20	1	0.65
Distance to nearest village		1.32	1	0.24
Village with 1km radius		0.016	1	0.89
Area of village within 1km radius		0.053	1	0.81
Rabbits		1.037	1	0.30
Corvids		0.29	1	0.58
Year		0.20	1	0.64
Slope		0.40	1	0.52
Plot type		0.40	1	0.050
Distance to vehicle accessible track		1.054	1	0.30
Age of plot		0.00006	1	0.99
Use by stone curlews since created		1.26	1	0.26
Presence of manure heaps		2.45	1	0.11

Table 6.10. Parameter estimates for logistic regression models relating the probability of plot occupancy for a first breeding attempt to disturbance variables alone

Disturbance variable	Year	Intercept	Regression coefficient	Residual deviance	df	p
Expected number of expected active responses per hour during settlement	2004	0.6408	-2.5708	70.31	1	0.0097
	2004	0.5586	-0.7263	72.38	1	0.031
Settlement disturbance event rate	2005	0.4185	-2.02195	80.26	1	0.048
	2005	0.4438	-0.8270	80.28	1	0.040
Expected number of expected active responses per hour during settlement	Combined	0.4858	-2.0234	152.51	1	0.0032
	Combined	0.4772	-0.7126	153.66	1	0.0061

Table 6.11. Performance of logistic regression models in classifying occupied and unoccupied plots assessed using AUC values from ROC curves.

Year	Model	AUC	SE	P	Figure
2004	Full with expected number of active responses	0.735	0.071	0.003	6.2
2004	Full with disturbance event rate	0.690	0.075	0.015	6.3
2004	Expected number of active responses only	0.677	0.074	0.024	6.4
2004	Disturbance event rate only	0.588	0.079	0.25	6.5
2005	Full with expected number of active responses	0.759	0.062	0.001	6.6
2005	Full with disturbance event rate	0.805	0.054	<0.001	6.7
2005	Expected number of active responses only	0.747	0.065	0.001	6.8
2005	Disturbance event rate only	0.684	0.070	0.014	6.9
Combined	Full with expected number of active responses	0.702	0.049	<0.0001	6.11
Combined	Full with disturbance event rate	0.728	0.046	<0.0001	6.13
Combined	Expected number of active responses only	0.671	0.051	0.001	6.10
Combined	Disturbance event rate only	0.614	0.053	0.034	6.12

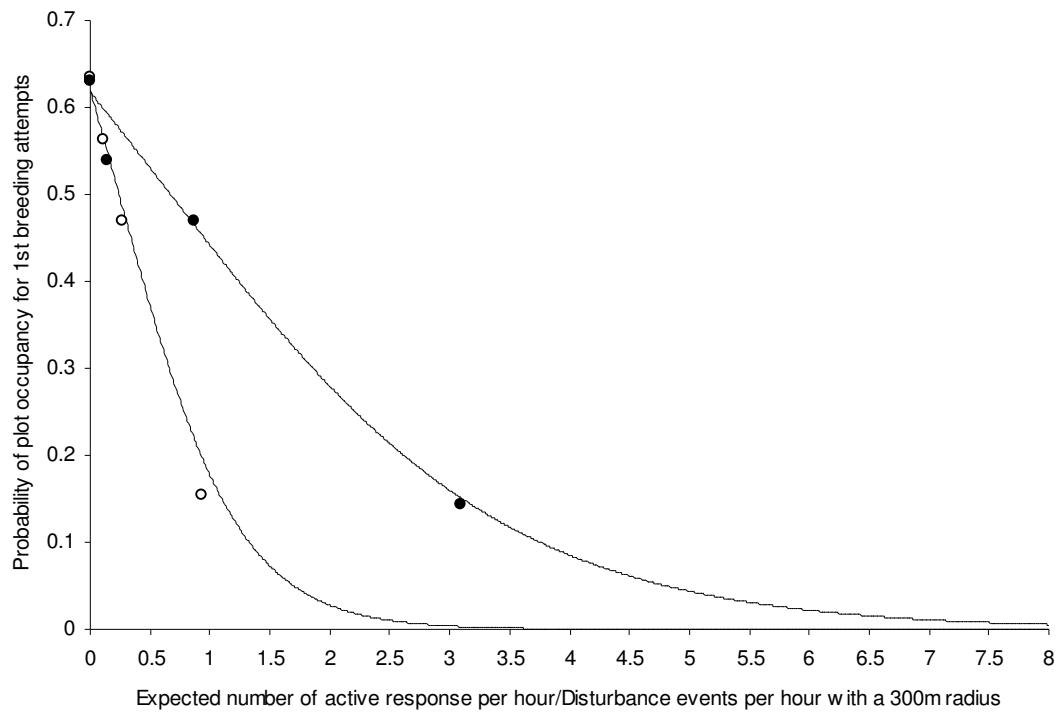


Figure 6.1. Probability of occupancy of nesting plots by stone curlews for first breeding attempts in relation to expected number of active responses per hour during the settlement period (---○---); and settlement disturbance event rate (—●—). The points are the proportions of occupied plots for bins of the disturbance variables and the lines are the logistic regression models fitted to the disaggregated data. Data from 2004 and 2005 breeding seasons are combined.

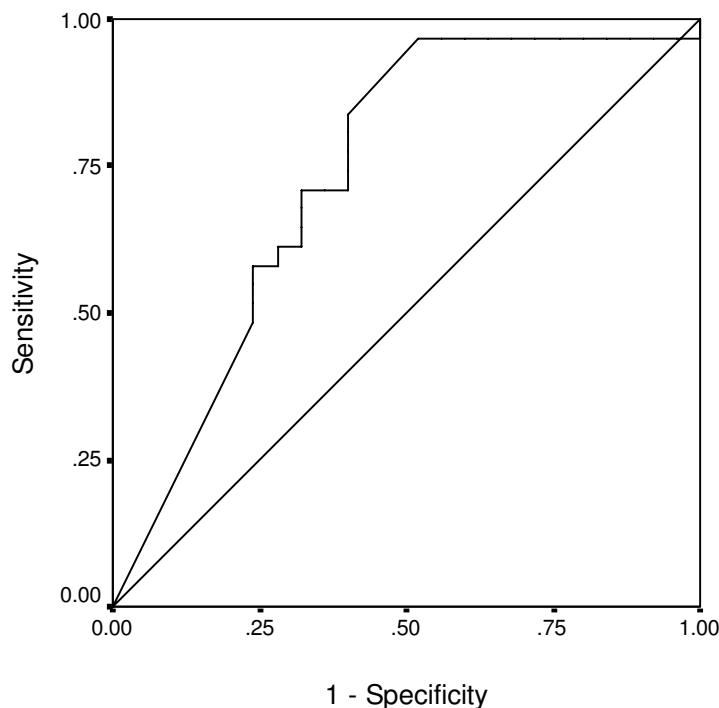


Figure 6.2. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2004 to the expected number of active responses per hour during settlement, and the presence of another occupied plot within sight (Table 6.4). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

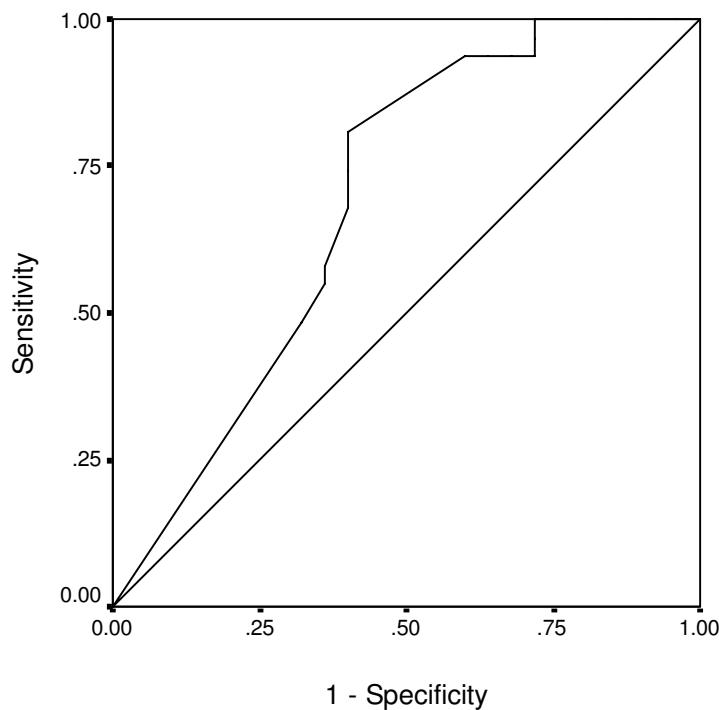


Figure 6.3. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2004 to the settlement disturbance event rate, and the presence of another occupied plot within sight (Table 6.5). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

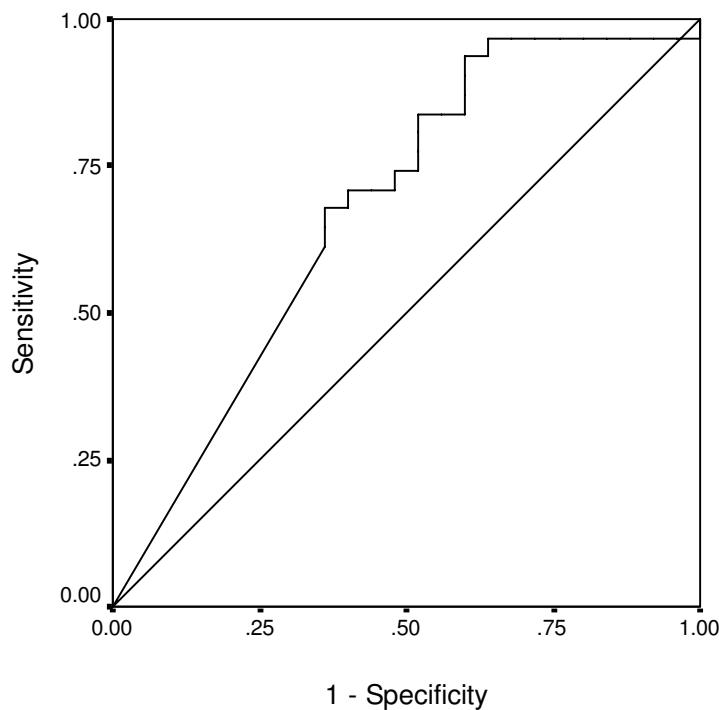


Figure 6.4. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2004 to the expected number of active response per hour during settlement (Table 6.10). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

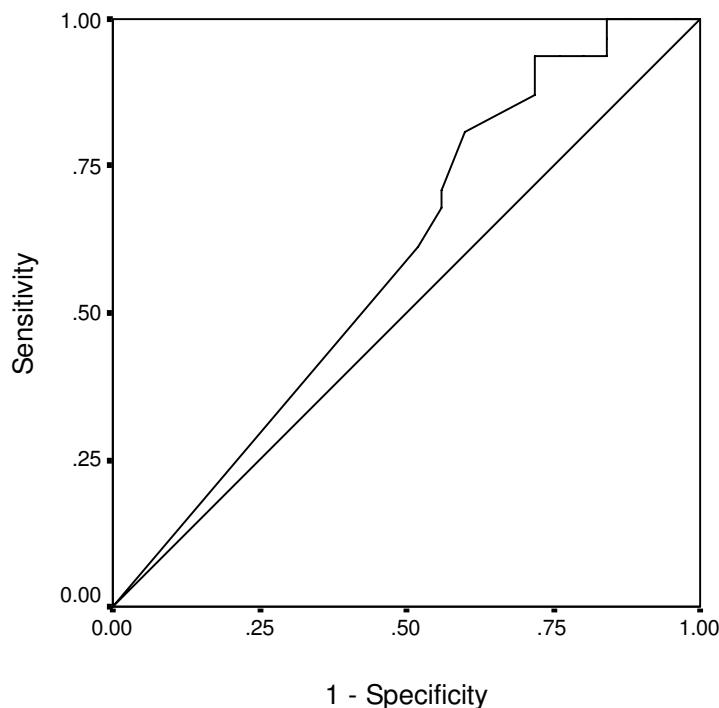


Figure 6.5. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2004 to the settlement disturbance event rate (Table 6.10). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

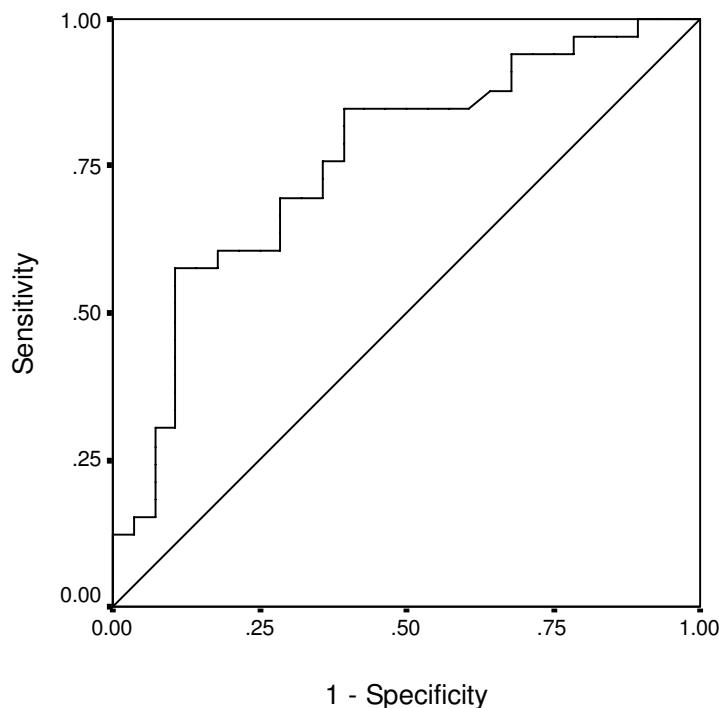


Figure 6.6. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2005 to the expected number of active responses per hour during settlement , the distance to the nearest woodland edge and the distance to the nearest A road (Table 6.6). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

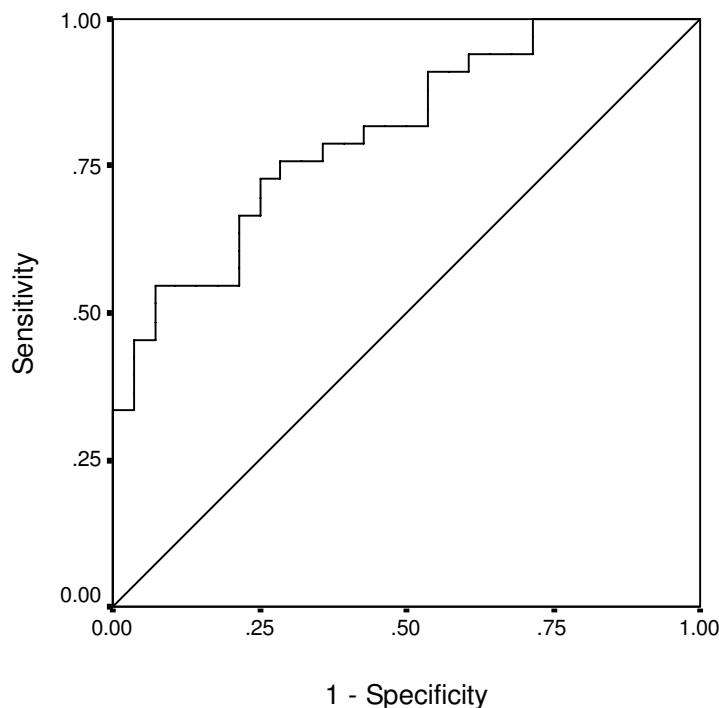


Figure 6.7. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2005 to the settlement disturbance event rate, the distance to the nearest woodland edge, the area of the plot, the length of A road within 1km radius and the distance to the nearest A road (Table 6.7). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

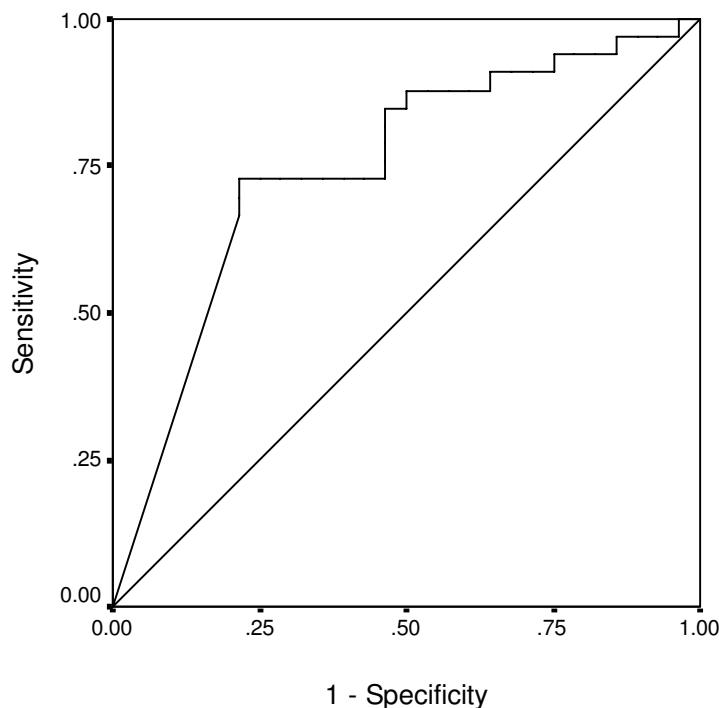


Figure 6.8. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2005 to the expected number of active responses per hour during settlement (Table 6.10). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

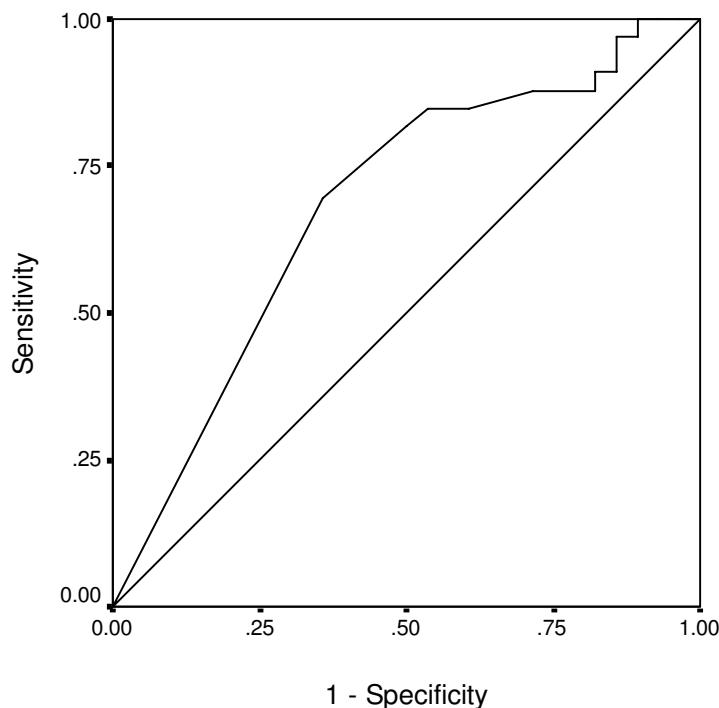


Figure 6.9. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in 2005 to the settlement disturbance event rate (Table 6.10). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

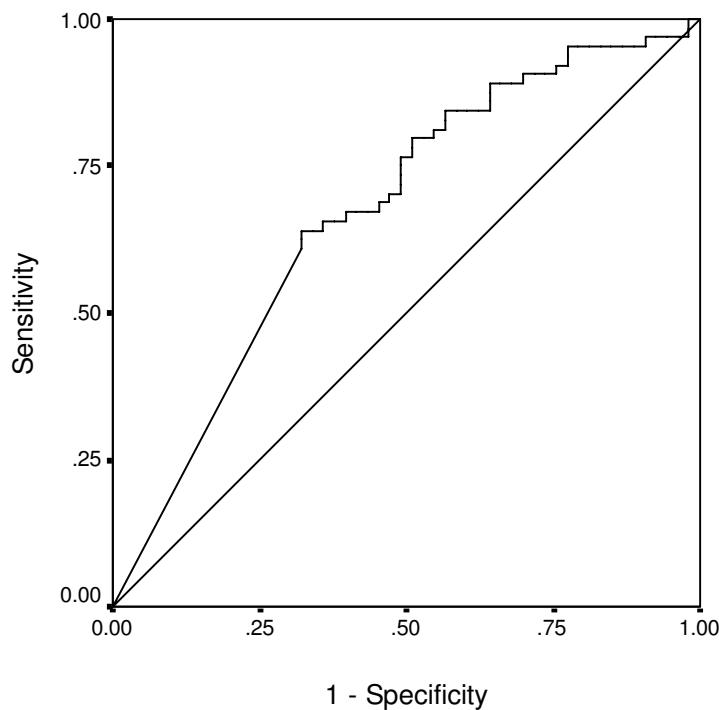


Figure 6.10. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in both years to the expected number of active responses per hour during settlement (Table 6.10). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event. The AUC value is 0.671.

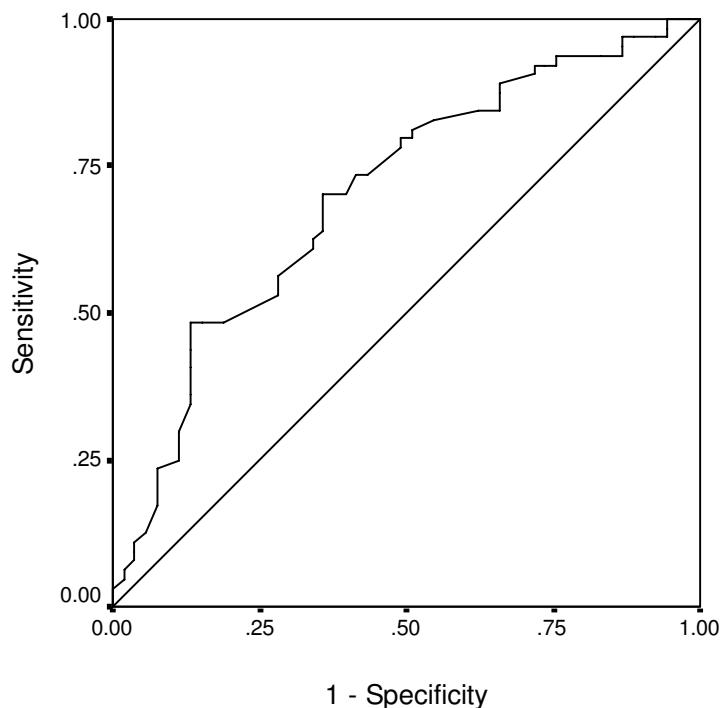


Figure 6.11. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in both years to the expected number of active responses per hour during settlement, the distance to the nearest woodland edge, and the distance to the nearest A road (Table 6.8). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event. The AUC value is 0.702.

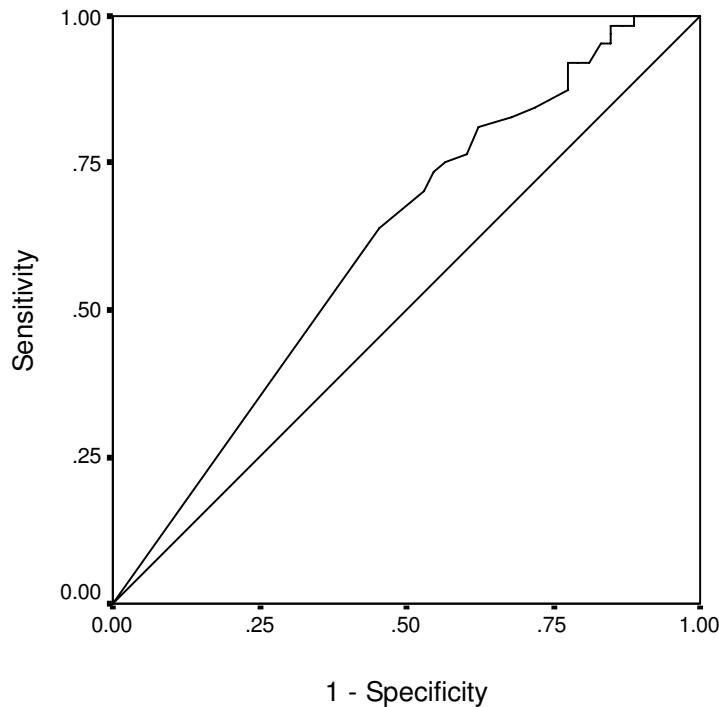


Figure 6.12. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in both years to settlement disturbance event rate (Table 6.10). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

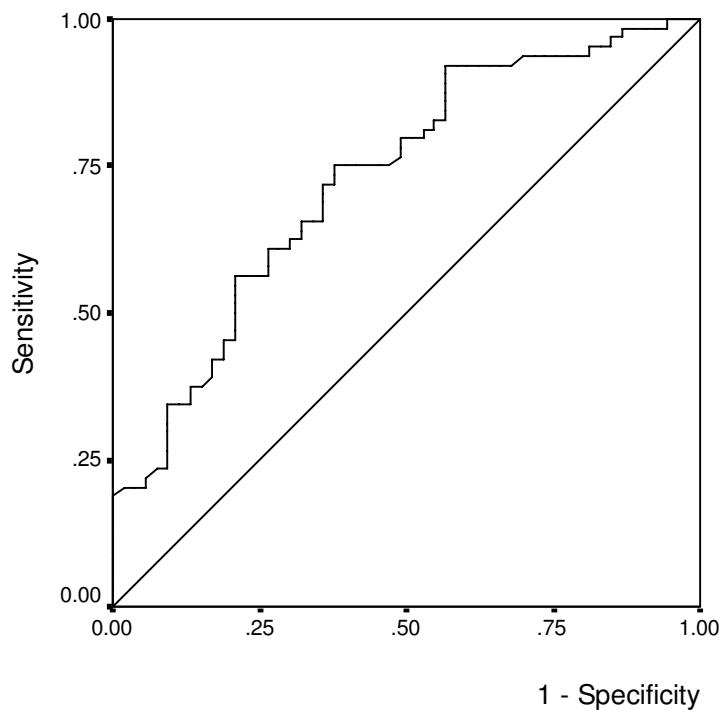


Figure 6.13. Receiver operating characteristics (ROC) curve used to assess the performance of the logistic regression models describing the probability of plot occupancy for first breeding attempts in both years to the settlement disturbance event rate, the area of the plot, the distance to the nearest A road and the presence of another occupied plot with visibility (Table 6.9). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

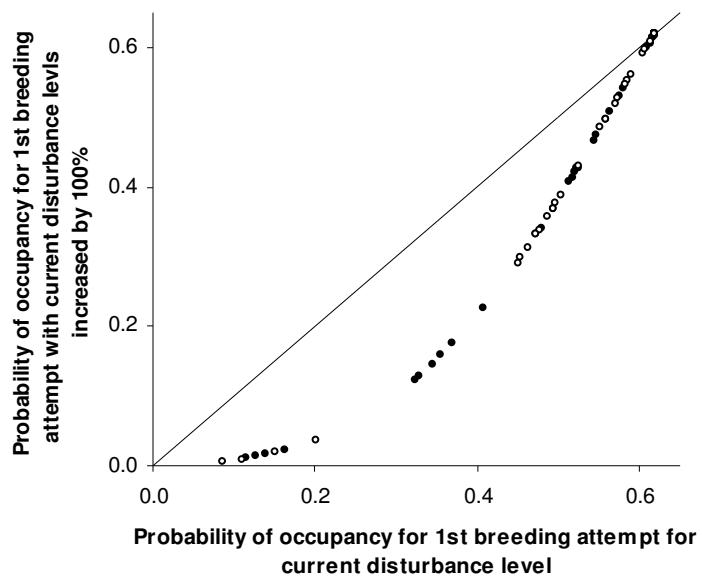


Figure 6.14. Projected change in probability of plot occupancy with a 100% increase in the current disturbance level at each site. Plots are shown separately for 2004 (●) and 2005 (○). There is a 9% reduction in the proportion of plots expected to be occupied with doubled current disturbance levels. The diagonal line through zero indicates where points would lie with no change observed.

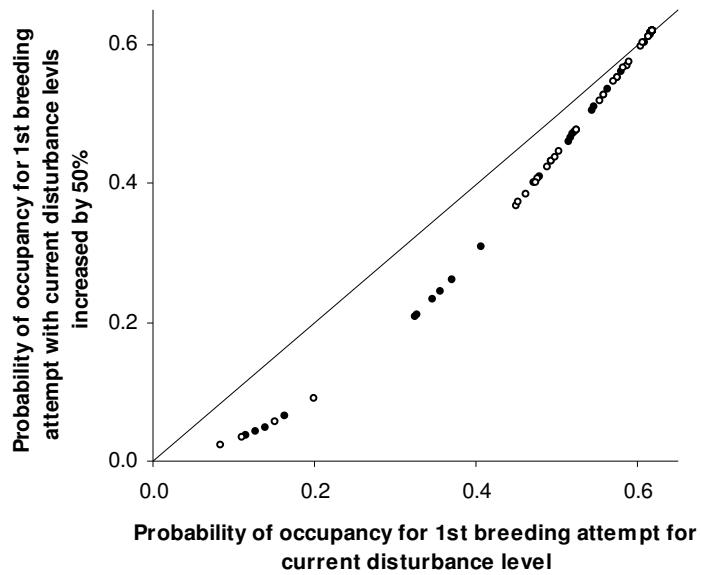


Figure 6.15. Projected change in probability of plot occupancy with a 50% increase in the current disturbance level at each site. Plots are shown separately for 2004 (●) and 2005 (○). There is a 5% reduction in the proportion of plots expected to be occupied with doubled current disturbance levels. The diagonal line through zero indicates where points would lie with no change observed.

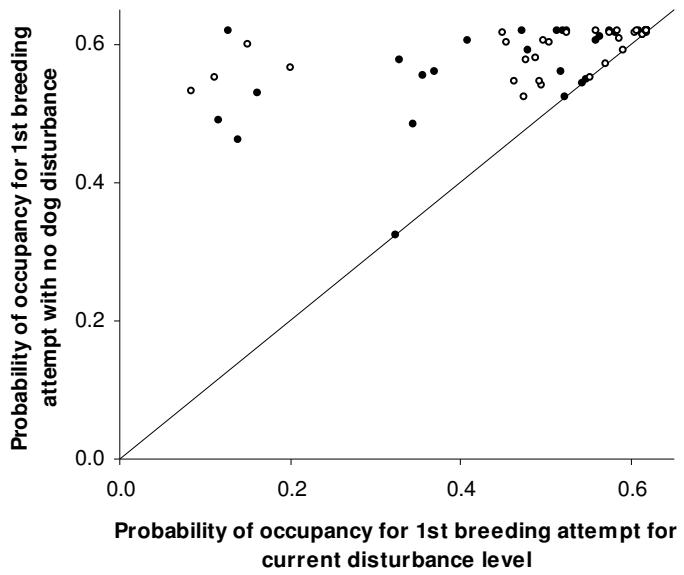


Figure 6.16. Projected change in probability of plot occupancy with the exclusion of dogwalkers at each site. Plots are shown separately for 2004 (●) and 2005 (○). There is a 10% increase in the proportion of plots expected to be occupied with exclusion of dog walkers. The diagonal line through zero indicates where points would lie with no change observed.

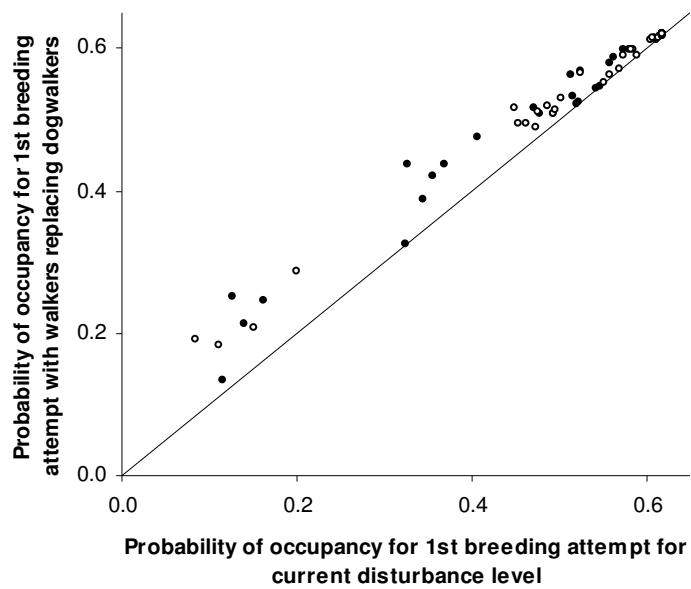


Figure 6.17. Projected change in probability of plot occupancy with the exclusion of dogs at each site but with walkers continuing to use the site. Plots are shown separately for 2004 (●) and 2005 (○). There is a 4% increase in the proportion of plots expected to be occupied with this scenario. The diagonal line through zero indicates where points would lie with no change observed.

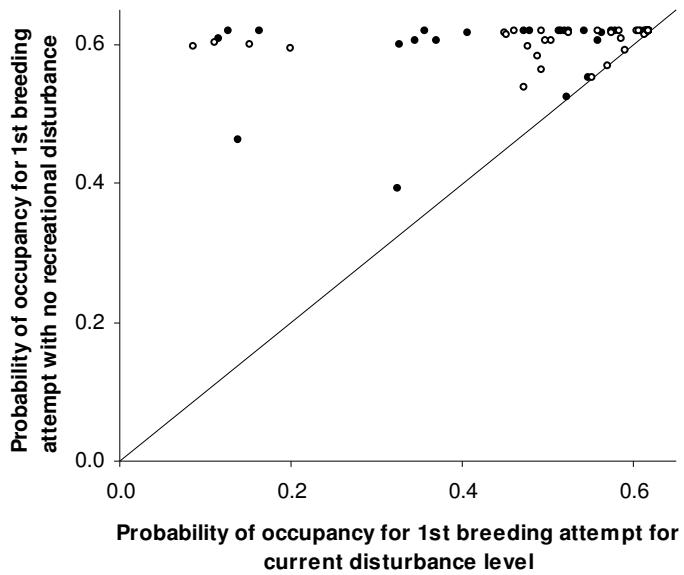


Figure 6.18. Projected change in probability of plot occupancy with the exclusion of recreational disturbance at each site. Plots are shown separately for 2004 (\bullet) and 2005 (\circ). There is a 11% increase in the proportion of plots expected to be occupied with this scenario. The diagonal line through zero indicates where points would lie with no change observed.

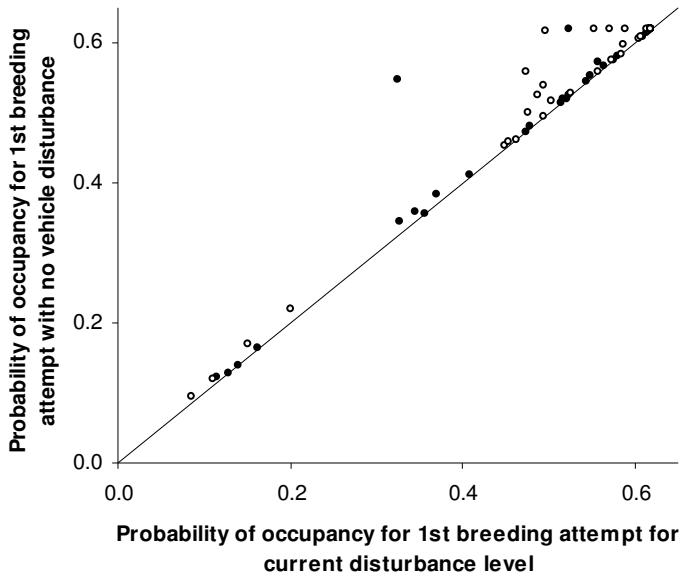


Figure 6.19. Projected change in probability of plot occupancy with the exclusion of vehicles at each site. Plots are shown separately for 2004 (●) and 2005 (○). There is a 2% increase in the proportion of plots expected to be occupied with this scenario. The diagonal line through zero indicates where points would lie with no change observed.

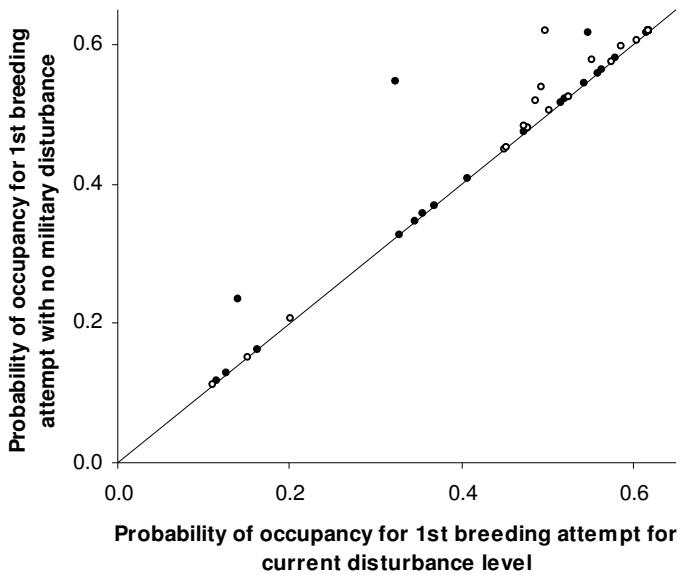


Figure 6.20. Projected change in probability of plot occupancy with the exclusion of military disturbance at each site on SPTA. Plots are shown separately for 2004 (●) and 2005 (○). There is a 2% increase in the proportion of plots expected to be occupied with this scenario. The diagonal line through zero indicates where points would lie with no change observed.

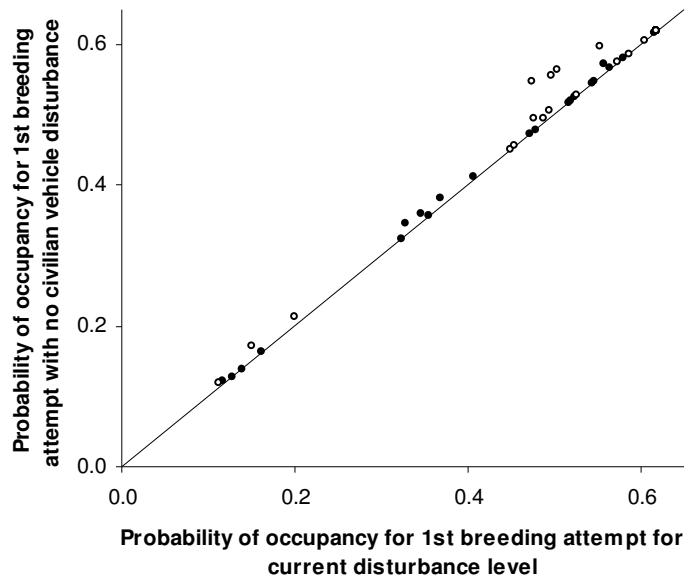


Figure 6.21. Projected change in probability of plot occupancy with the exclusion of civilian vehicle disturbance at each site on SPTA. Plots are shown separately for 2004 (●) and 2005 (○). There is a 2% increase in the proportion of plots expected to be occupied with this scenario. The diagonal line through zero indicates where points would lie with no change observed.

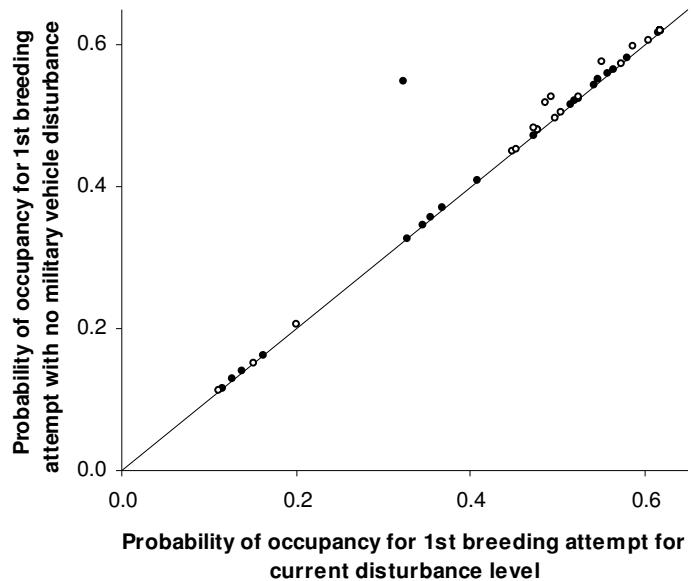


Figure 6.22. Projected change in probability of plot occupancy with the exclusion of military vehicle disturbance at each site on SPTA. Plots are shown separately for 2004 (●) and 2005 (○). There is a 1% increase in the proportion of plots expected to be occupied with this scenario. The diagonal line through zero indicates where points would lie with no change observed.

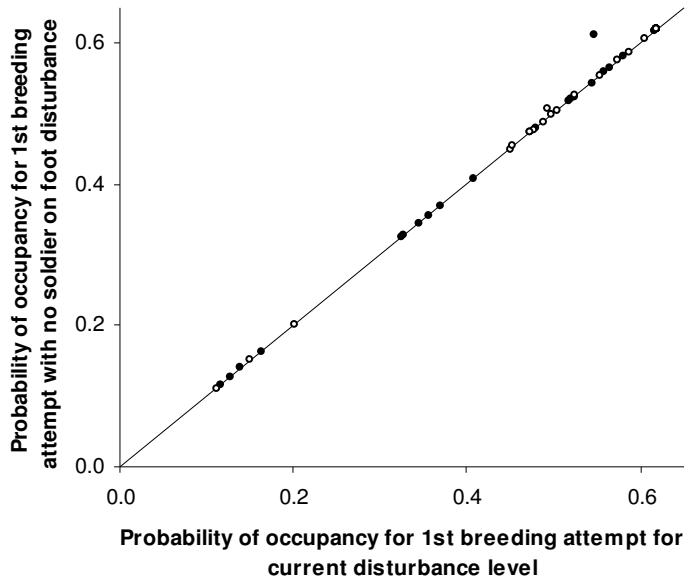


Figure 6.23. Projected change in probability of plot occupancy with the exclusion of soldiers on foot at each site on SPTA. Plots are shown separately for 2004 (●) and 2005 (○). There is a 0.2% increase in the proportion of plots expected to be occupied with this scenario. The diagonal line through zero indicates where points would lie with no change observed.

7 Effects of human disturbance on the breeding success of stone curlews in Wessex

7.1 Summary

Human disturbance has been observed to affect the productivity of birds. Nest survival, chick growth, chick survival and recruitment into the breeding population are among the demographic rates which have been reported to be adversely affected by human disturbance. In this study of stone curlews in Wiltshire and Hampshire over a two year period, chicks grew more slowly on sites with disturbance but this had no significant effect on chick survival to fledging. No other significant effects of disturbance on breeding success were observed. This either suggests that there are few adverse impacts of disturbance on breeding success, or it could be a product of stone curlews already selecting against the most disturbed plots and so variation in disturbance levels are low and any impacts on breeding success are not apparent.

7.2 Introduction

Variations in the breeding success of birds, sometimes leading to changes in population size, are caused by many factors. Components of breeding performance that vary include clutch size (Amat *et al.*, 2001; Robertson, 1995); egg size (Amat *et al.*, 2001, Robertson, 1995), nest survival (Seymour *et al.*, 2003; Bealey *et al.*, 1999), chick growth rate (Yalden and Yalden, 1991) and chick survival (Bealey *et al.*, 1999). Whilst reduced nest success or clutch sizes are clear drivers in determining overall productivity, other factors have more indirect consequences.

Chicks hatched from large eggs tend to be more likely to survive fledging than conspecific chicks from small eggs, particularly in precocial species which feed for themselves shortly after hatching (Amat *et al.*, 2001; Robertson, 1995). Larger eggs often contain an increased nutrient reserve in the yolk which may allow chicks better thermoregulation and therefore more foraging activity which can then lead to increased growth rate, particularly in the first few days after hatching. Few studies have shown an effect of egg size on chick growth after this period or any correlation with fledging success, although one study found an effect on recruitment of Kentish plover *Charadrius alexandrinus* chicks (Amat *et al.*, 2001).

Chick growth rate to fledging has been shown to correlate with long term chick survival (Park *et al.*, 2001) and recruitment into the breeding population (Stienen and Brenninkmeijer, 2002).

Chick growth has also been found to correlate with size and condition when adult, which can then affect fecundity (Stienen and Brenninkmeijer, 2002).

Aspects of reproductive performance might be determined by factors associated with individual chicks (Christians, 2002), their parents, or external factors at the breeding site, such as food supply, habitat quality (Donald *et al.*, 2002), weather patterns (Yalden and Yalden, 1990), predator abundance (Schauer and Murphy, 1996; Sockman, 1997) and human disturbance (Hockin *et al.*, 1992).

The effects of human disturbance on reproductive parameters are numerous. Reduction in foraging ability prior to laying by the female, caused by human disturbance, can result in a sub-optimal clutch being laid, leading to a reduced chance of successful hatching (Amat *et al.*, 2001). Nests can fail as a direct result of human disturbance through trampling by people or pets or being driven over by a vehicle (Woodfield and Langston, 2004). Disturbance can also cause accidental trampling or displacement of eggs by the parent birds if they are flushed off nests, as found in a study of guillemots *Uria aalge* (Schaur and Murphy, 1996). Chick growth and survival can be reduced by disturbance if adults are kept away from nests, as found in studies of herring gull *Larus argentatus* (Hunt, 1972) and brown pelican *Pelecanus occidentalis* (Anderson and Keith, 1980); or if the time available for foraging is reduced by the need to hide, as seen in the case of golden plover *Pluvialis apricaria* (Yalden and Yalden, 1990). A reduction in foraging by chicks, or a reduction in food provisioning by the adults, could affect chick condition, making them more susceptible to severe weather or predation (Fernandez and Azkona, 1993). In addition, reduced brooding by adults as a result of disturbance could lead to reduced chick survival particularly in poor weather (Flemming *et al.*, 1988). Chicks may also be separated from parents as a result of fleeing from disturbance (Burger, Gochfeld and Niles, 1995). Additionally, poor condition of chicks as a result of human disturbance before fledging, could lead to a reduction in adult survival or recruitment (Amat *et al.*, 2001). Where disturbance exceeds a threshold, parent birds may abandon eggs or chicks. This has been observed in brown pelicans (Anderson and Keith, 1980), piping plovers *Charadrius melanotos* (Anderson, 1988), and black-crowned night herons *Nycticorax nycticorax* (Stauss, 1990).

Birds may also suffer physiological stress in response to disturbance. Physiological changes such as increased heart rate (de Villiers *et al.*, 2006), lowered or less-regulated body temperatures (Boyd and Sladen, 1971, Regal and Putz, 1997) and increased corticosterone levels (Fowler,

1993) have been observed in several species. Energy budgets may also be affected by disturbance by, for example, increasing energy expenditure through flushing (Huppop and Gabrielsen, 1998). These effects of disturbance are more subtle and harder to measure but may have long-term impacts on body condition and hence survival, fitness and productivity (Huppop 1995, Huppop & Gabrielsen 1998).

The main mechanisms underlying failures at the nest stage are nest predation, and the influence of human disturbance on predation risk can be important at both the egg and chick stages (Giese, 1996). The effect of disturbance on predation risk may arise because disturbance affects the behaviour of the parent birds or the predator or both. Eggs may be predated because adults are kept away from the nest by human disturbance, as seen in observations of guillemot (Schauer and Murphy, 1996) and eider *Somateria mollissima* (Sockman, 1997). Alternatively, human activity in an area may keep predators away from nest sites and therefore decrease predation (Miller and Hobbs, 2000; Liley, 1999), or attract predators and so increase predation (Jokimaki and Huhta, 2000; Sieving, 1992; De Santo and Willson, 2001). Additionally, pet dogs may directly depredate eggs and chicks of ground nesting species (Nol and Brooks, 1982; Pienkowski, 1984; Woodfield and Langston, 2004).

Studying the effects of disturbance on components of productivity is complex because other factors influence breeding parameters and effects of human disturbance are likely to be correlated with them and therefore masked or given spurious apparent importance. For example egg size and quality is usually correlated with the age, experience, condition and other individual characteristics of breeding females (Christianss, 2002) and weather variables can affect chick growth and survival (Yalden and Yalden, 1990). Female age and experience and local weather might well differ among sites or years and obscure real effects of disturbance. The dominant mechanism inducing changes in breeding parameters is likely to vary between and within species, and with changes in other variables at the breeding site (Sidaway, 1990).

Stone curlew nest success, chick growth rate and chick survival were found to vary among years at Porton Down in Wiltshire (Bealey *et al.*, 1999). There were correlations of breeding success and its components with the abundance of rabbits (the main grazer of the birds' habitat), weather and the abundance of predators. In an analysis of 16 years of stone curlew data from the Breckland sub-population and including measures of distance to roads, weather, female age, year

and lay date, Day (2003) found few significant correlates of variation among pairs and years in reproductive performance and no effects of disturbance from vehicles on major roads.

In this study I found that stone curlews avoid disturbed sites even when other measures of habitat quality appear to be optimal (Chapter 6 and Chapter 8). This may be an effect of current high habitat availability and less disturbed alternatives available and so these are chosen because there is a *perceived risk* of disturbance (Beale and Monaghan, 2004), arising if birds show predator avoidance behaviour to humans and their pets and vehicles even if these are not really predators and pose no threat to them. There may be no effects of disturbance on breeding success or survival and so avoidance of disturbed areas may be psychological. In this situation, stone curlews that are displaced might still suffer lower breeding success than would otherwise be the case. This might occur in several ways. Displaced pairs might lose time for breeding because of the displacement, they might move to lower quality or more predator-rich habitat than that at the disturbed site or they might face more interference with breeding and foraging by other stone curlews because of a shortage of sites. Alternatively, there may be sufficient high quality habitat available at alternative less disturbed sites for displacement from disturbed sites not to adversely affect breeding success. If this is the case, then disturbance may not be a concern at the population level. However, disturbance might become important in the future if the bird population grows or the amount of habitat diminishes. Stone curlews might eventually be forced to breed in areas with poor habitat or refrain from breeding. Therefore, with changes in countryside access and a growing stone curlew population, it is important to explore the consequences of disturbance. In this chapter I assess the effects on breeding success of disturbance at the sites where stone curlews settle to breed.

7.3 Aims of chapter

The aim of this chapter is to:

- Examine patterns of egg size, nest failure rate, causes of nest failure, chick growth, chick survival and recruitment in relation to disturbance levels and other factors at breeding sites.

7.4 Methods

Sites were selected using the method described in section 2.4.1. Stone curlew surveys, nest finding, egg measurements, chick measurements and monitoring are described in section 2.4.2. Disturbance surveys followed the protocol in section 2.4.3 and disturbance event rate was derived using the method in 2.5.1. The expected rate of active responses was calculated for sites using

the models from Chapter 4 and the methods in Chapter 5. Habitat variables are described in 6.4.1.

7.5 Data Analysis

Variables that may be important in influencing aspects of breeding parameters are shown in Table 7.1. Variables were only tested if their influence was biologically plausible and the amount of available data was adequate.

7.5.1 Egg size

Multiple linear least squares regression was used to model the variation in egg size with potential explanatory variables (Table 7.1). Full models were fitted with all explanatory variables and Minimal Adequate Models (MAMs) selected using the backward stepwise elimination method (Crawley, 2002).

An egg size index which has been used in previous stone curlew studies was calculated from the length of the egg multiplied by the square of the width at the widest point (Day, 2003). For each nest, the egg size index was calculated separately for each egg and a mean taken as the egg size for this nest. Only nests where two eggs were measured were used in egg size analyses.

Female age was known for only 20 pairs with two egg nests but given the importance of female age in determining egg size (Day, 2003), I modelled data sets with and without female age separately. Additionally, given that egg size can decline with seasonal factors, modelling was also performed separately for first nesting attempts and using all nesting attempts in a season.

7.5.2 Nest success

Daily failure probability of nests at the egg stage (Mayfield, 1975) was modelled as function of explanatory variables using multiple logistic regression (Aebischer, 1999) (Table 7.1). The dependent variable was the binary variable failure or non-failure and each day on which the nest was monitored (exposure day) was taken to be a binomial trial. The model was fitted in S-Plus with a logit link, binomial error and the exposure period in days was entered as the binomial denominator. Nest failure was assumed to occur half-way between the last visits. Nest survival for first breeding attempts and all breeding attempts were modelled separately.

Minimal adequate models were selected using the backward elimination method from assessment of deletion tests (Crawley, 2002). The reduction in residual deviance caused by entering an explanatory variable was treated as a likelihood ratio test and its significance assessed by comparing it with the χ^2 distribution with the appropriate degrees of freedom.

The probability of stone curlews deserting nests was modelled as a function of explanatory variables (Table 7.1) using logistic regression, in which the binary response was desertion or no desertion.

7.5.3 Chick growth

An index of chick growth rate was calculated as the observed weight when ringed divided by the expected weight at this age. Expected weight was calculated from age using a Von Bertalanffy growth curve previously fitted to weights of stone curlew chicks of known age that were known to have survived to fledging by Day (2003):

$$\text{Weight} = A (1 - e^{-k(age - t)})^3$$

Where:

A (asymptotic chick weight) = 472.698

t = -10.417

k = 0.0470

Multiple linear regression was used to model growth rate index in relation to appropriate independent variables (Table 7.1). Chick growth is likely to be dependent on the rank of the individual in the brood. For example, single chicks may grow faster in the absence of sibling competition. In broods of two chicks there is also usually a dominant “alpha” chick that grows faster than its sibling, the “beta” chick. There was not enough data to model these chick types separately, therefore chick type was specified as a three level factor in the model (Table 7.1).

7.5.4 Chick fledging rate

Chick fledging rate was defined as whether any chicks fledged from a nest or not. Fledging rate was modelled with potential explanatory variables (Table 7.1) using multiple binomial logistic regression with fledging or not as the binary response variable. Fledging success was defined as chicks observed in autumn roosts or away from nest sites, or known survival beyond 42 days.

7.5.5 Chick survival

Chick survival was represented as the number of chicks fledged as a proportion of those known to hatch. Survival rate was modelled using multiple regression with a binomial error structure. Again, fledging success was defined as chicks observed in autumn roosts or away from nest sites, or known survival beyond 42 days.

7.6 Results

7.6.1 Description of breeding seasons

There were 122 known breeding attempts in my study area over the two years of data collection (2004 – 54, 2005 – 68). Of these, 82 were first breeding attempts (2004 – 40, 2005 – 42). Only 29.27% (n=24) of first nesting attempts and 26.23% of all nesting attempts (n=32) successfully fledged one or more chicks. The remainder were either deserted at the egg stage, predated at the egg stage or failed at the chick stage (Figure 7.1).

Of the 50 nests that were predated at the egg stage, two were attributed to corvid predators and six were attributed to mammalian predators from signs left at the nest. However, in the remainder of cases eggs were taken from nests with no signs left as to the identity of the predator. Therefore, no further attempt can be made to attribute predation to predators.

7.6.2 Egg size

a) First breeding attempts

Using the data set where female age was known (n=20), there was a significant effect of female age on egg size for first breeding attempts but egg size was not significantly affected by year, first egg date, the amount of suitable feeding habitat within a 1km radius of the nest site, or any of the disturbance variables (Table 7.2). The effect of female age was linear (Figure 7.2) with older birds laying larger eggs. The model was still significant even when the small egg outlier laid by a first year bird is removed ($R^2=0.283$, n=19, p=0.019).

Using the larger data set without female age, no variables entered into the model had a significant effect on egg size in first clutches, suggesting that female age is the most important factor determining egg size.

b) All nesting attempts

Using all nesting attempts for the two years (including replacement clutches and second broods) for the data set with female age, the minimal adequate model (Table 7.3) describing egg size included female age, first egg date (Figure 7.3) and the area of suitable feeding habitat within 1km (Figure 7.4). There were no significant effects of year, roads or the disturbance variables on variation in egg size.

Using the full data set, excluding female age, the minimal adequate model of egg size included first egg date only (Table 7.4).

7.6.3 Nest success**a) First nesting attempts**

The mean daily nest survival rate for first nesting attempts was 0.9594, equating to an overall nest survival rate over the incubation period of 59.0%. Using all first nesting attempts data there was a significant difference in daily survival rates between nests in arable and grassland habitats (Table 7.5). The daily survival rate for plots situated in grassland was 0.9467, which is equivalent to a probability of surviving the incubation period of 48.0%. Those nesting on plots within arable had a daily nest survival rate of 0.9835, which is equivalent to a probability of surviving the incubation period of 80.0%.

b) All nesting attempts

The mean daily nest survival rate for all nesting attempts combined was 0.9582, which is equivalent to an overall nest survival rate over the incubation period of 58.5%. Using all data combined there was also a significant difference in daily survival rates between arable and grassland habitats (Table 7.6). Stone curlew breeding habitat situated in grassland had a mean daily survival rate of 0.9480, which is equivalent to a probability of surviving the incubation period of 51.0%. Those nesting on plots within arable had a daily nest survival rate of 0.9819, which is equivalent to a probability of surviving the incubation period of 77.0%. There was also a significant effect of the number of corvids on daily nest survival, with increasing corvid index relating to a decrease in daily nest survival probability.

7.6.4 Desertions

There were 12 incidents of stone curlews deserting nests before the end of the incubation period. Desertion was more likely if the female appeared to have laid a single egg (Table 7.7)

7.6.5 Chick fledging rate

Chicks were more likely to fledge from nests where egg sizes had been larger (Figure 7.5). Additionally, nests on arable plots were significantly more likely to fledge chicks (Table 7.8).

7.6.6 Chick survival

None of the potential explanatory variables were associated with chick survival.

7.6.7 Chick growth

Chick growth was affected by year, hatch date (Figure 7.6) and whether the habitat was disturbed or not (Table 7.9). Chicks born later in the season grew faster, as did those on plots that were not disturbed. There was also a significant interaction between year and hatch date.

Using the reduced dataset where the parental age is known there was no effect of parental age on chick growth ($F=1.8$, $df=1,39$, $p=0.1875$).

7.6.8 Timing of first clutches

The mean first egg date across two years of data collection was the 28 April (range 31 March – 18 June). However, first egg dates were significantly different between the two study years (Table 7.10). In 2005, the mean date was 23 April (range 31 March – 10 June) whilst in 2004 the mean date was 3 May (range 5 April – 18 June). Additionally, first egg date also increased with distance from A road (Figure 7.7).

7.6.9 Replacement nests

First nesting attempts that failed at the egg stage were more likely to be replaced (where habitat suitability remained unchanged) if nests were initiated earlier in the season (Table 7.11 and Figure 7.8). Additionally, pairs further from A roads were likely to replace first nesting attempts failing at the egg stage (Figure 7.9).

There was not a large enough sample size to examine replacement nests after chick stage failures.

7.6.10 Second clutches

There was only one pair that produced a second brood after successfully fledging chicks from a first brood so no analyses were possible to determine factors associated with producing second broods.

7.6.11 Recruitment

Recruitment could not be adequately assessed due to the short term nature of the project. Stone curlews usually nest for the first time at age two so there may have been recruitment of chicks born in 2004 to the breeding population in 2006. However, only one 2004 chick from my study area was proved to breed in 2006. There was also one chick from 2004 recruited in 2005 and one chick from 2005 recruited in 2006.

7.7 Discussion

Being a ground nesting species, the stone curlew is vulnerable to nest predation by mammals, though it can drive away small predators such as stoats with some success (R.E. Green, pers. comm.). Corvids are probably also significant egg predators, though nest camera and temperature logger studies indicate that egg predation by foxes and badgers may predominate (E. Taylor and R.E. Green pers. obs). Almost 50% of nests initiated in this study were thought to have been predated at the egg stage, although the predator could not be identified in most cases. Despite high levels of predation, the long breeding season means that replacement nests are common.

Female age was the strongest influence on egg size, as reported by Day (2003) using a considerably larger dataset of stone curlew breeding attempts in the Brecks sub-population. In my study the relationship with age appears linear with older female stone curlews producing significantly larger eggs. However, Day (2003) observed a quadratic relationship where there was a peak in egg size at age 7-8, followed by a decrease, as observed in *Larus* sp. (Sydeman and Emslie, 1992) and *Diomedea* sp. (Weimerskirch, 1992). The data in my study did not contain any birds older than eight and so it is possible that a peak and decline pattern would have been evident with a larger sample size.

There is evidence from many other studies that egg size increases with age (or experience) and body mass of the female bird (Hipfner *et al.*, 1997; Robertson *et al.*, 1994), including a study of a species in the same order as the stone curlew, the semipalmated sandpiper *Calidris pusilla* (Gratto

et al., 1983). An intuitive hypothesis is that older females are in better reproductive condition and can produce larger eggs (to benefit the survival of chicks) however, it has been found that female body mass, size or condition variables can explain less than 20% of the variation in egg size within a species (Christians, 2002). A factor which was unmeasured in this study, but may be important in explaining variation in egg size, is weather. In other bird species, correlations between ambient temperature during egg formation and egg size yield mixed results including positive (Nager and Zandt, 1994), negative (Willias and Cooch, 1996) and no effect (Robertson, 1995).

As previously reported by Day (2003), egg size declined with first egg date when the full dataset was used. This was probably not because young birds were laying later in the season and producing smaller eggs, as suggested by Hill (1984), because as also found by Day (2003), the effect of first egg date remains in the model when the effect of female age is allowed for. In roseate terns *Sterna dougallii* egg size increased with first egg date (Ramos, 2001) whilst in tufted ducks *Aythya fuligula* a decrease was shown (Hill, 1984). A relationship of egg size to date was not apparent when only first clutches were examined. Hence, the trend may arise because females have quite a long time between arrival from migration and laying the first clutch to accumulate food reserves, whereas replacement clutches are generally produced in a short time.

Egg size tended to be larger in areas where there was a larger amount of suitable feeding habitat within 1km radius of the nest site. Stone curlews are known to forage at night at distances of 1km or more (Green, Tyler and Bowden, 2000) and so a larger amount of feeding habitat may allow the female to accumulate food reserves rapidly, which may then be expressed in the size of eggs produced. This relationship between habitat quality and egg size has also been observed in lapwings *Vanellus vanellus* (Blomqvist and Johansson, 1995). Additionally, increases in egg size as a result of supplementary feeding or enhanced food quality have also been observed in several species of passerines (Ramsey and Houston, 1997; Williams, 1996) and water birds (Eldridge and Krapu, 1988; Hill, 1988). However, the relationship may also be a product of these sites being of a higher quality and occupied by the fittest pairs, which may then produce larger eggs (Blomqvist *et al.*, 1997).

There was no evidence for disturbance affecting egg size either for first breeding attempts or all attempts combined. Lack of a relationship between egg size and disturbance is not surprising if other factors are of greater importance. Disturbance could cause less foraging and more stress to

females in the egg development period. However, as stone curlews mostly forage at night, they would probably not be affected by disturbance in this way.

Nests had a greater probability of failing if they were on plots within grassland rather than arable crops. Data from nest temperature loggers show the majority of failures occur at night or in the early hours of the morning before light (E.C. Taylor pers obs., R.E. Green pers. comm.), so it is thought that the majority of predators are mammals. Therefore, the relationship between nest failures and the habitat around plots is explicable because mammalian predators are probably less likely to visit a plot surrounded by a dense arable crop than short grassland because of the physical structure of the vegetation. Also, there is probably more food of other kinds (rabbits, earthworms, dung beetles, other nests) on grassland than arable land so predators are likely to spend more time there foraging. Unfortunately, it was not possible to obtain accurate measurements of mammalian predator activity in this study so the relationship between mammalian predator abundance and nest failure could not be assessed. There was an association between nest survival and the index of corvid predator abundance, a relationship also found by Bealey *et al.*, (1999) on Porton Down, Wiltshire. However, in my study, corvids were only definitely attributed to two nest failures. The association between corvids and nest failure may be a true effect or it is possible that corvid abundance is a surrogate for general predator control activity by gamekeepers and so higher levels of corvids may also mean higher levels of mammalian predators. Where disturbance keeps birds away from nests it is likely the main predator would be corvids as they would be more likely than mammals to be around nest sites at the time of disturbance, and they are also less wary of human activities (Knight *et al.*, 1987).

Stone curlew nest success has been shown to be related to the numbers of rabbits on semi-natural chalk grassland at Porton Down (Bealey *et al.*, 1999), possibly because rabbits provide optimum habitat conditions on chalk grassland or foxes may spend less time searching for stone curlew nests when rabbit numbers are high. However, in my study, the rabbit index used was not related to nesting success. This is possibly a result of rabbits being less abundant in my study area than at Porton Down and also less associated with stone curlews on plots because plots are unvegetated and less suitable for feeding by rabbits.

From the small number of observed desertions, the only significant factor determining whether a nest would be deserted appeared to be the number of eggs laid, with stone curlews laying a single egg more likely to desert a nest. If single egg clutches are laid by females in poorer condition this

suggests that desertions may be a result of low quality eggs being laid. Alternatively, some one egg clutches might have started with two eggs and had one egg taken by a predator. This might lead the pair to desert later. Although no relationships were found in this study, it is possible that very high incidences of disturbance could cause desertion. Adults may choose to abandon nests if they are constantly forced off nests and embryo survival suffers (Yasue and Dearden, 2006). Alternatively, as birds probably perceive human disturbance as a risk of predation (Frid and Dill, 2002), constant disruption from incubation may make adults perceive a greater predation risk to themselves from incubation and increase the likelihood of desertion (Ghalambor and Martin, 2001). Disturbance was considered to be the direct cause of desertion in two cases over two years where military training activities were particularly intense for prolonged periods. Therefore, there may be a risk of desertion from high levels of disturbance which my study did not detect.

Nests with larger eggs were more likely to produce chicks that survived to fledging. However, no relationships were found between the proportion of hatched eggs that produced fledged young and any explanatory variables. It is suggested that larger eggs only produce an advantage to chicks for the first few days (Christians, 2002; Williams, 1994). This is especially the case in waders that leave the nest soon after hatching and need egg nutrient reserves before they learn how to feed independently. Larger eggs did not produce chicks that had grown faster at the time when they were ringed. However, as chicks were mostly all 14 days or older when ringed, an early advantage of large egg size may have been obscured by effects operating later. Parental quality may be more important in determining chick growth and it is difficult to separate the effect of egg size from that of parental quality (Williams, 1994). In a study of lapwing *Vanellus vanellus* chicks, those hatched from large eggs survived better than those from smaller eggs but this was not independent of parental quality as fledging success also increased with parental age or experience. If parental attributes such as age and experience correlate with egg size, parental quality rather than egg size may affect offspring fitness to a greater extent than other factors (Blomqvist *et al.*, 1997). With stone curlews, as chicks from larger eggs are more likely to be from older females the effect may be a product of increased parental quality rather than a direct result of egg size. Age of female had no significant effect on chick survival but the sample size was small.

Chick fledging rate was also dependent on whether the plot was within grassland or an arable crop. Nests in arable crops were more likely to produce chicks that survived to fledging. This is

likely to be because of differences in predator use of the two habitats as discussed for nest survival.

Chick survival was not related to chick growth, as was found in another study of stone curlews in Wiltshire (Bealey *et al.*, 1999). Additionally, despite relationships between chick survival and human activities in other studies (e.g. Dowling and Weston, 1999, Flemming *et al.*, 1998; Strauss, 1990; Goldin and Regosin, 1998, Ruhlen *et al.*, 2003), no effect of disturbance was found.

There was variation between years and with hatch date in chick growth, probably relating to weather variables. Stone curlews chicks are known to grow faster in wetter, warmer springs where food availability (especially of earthworms) may be higher (Day, 2003). Additionally, chicks on disturbed sites grew slower than those on sites with no disturbance. However, there was no difference in fledging probability or the proportion of eggs hatched that fledged on disturbed and undisturbed sites. Stone curlews mostly feed at night (Green, Tyler and Bowden, 2000) but during chick rearing a larger proportion of time is spent feeding during the day (Green, Tyler and Bowden, 2000, E. Taylor pers. obs). Therefore, disturbance could interrupt daytime feeding and lead to reductions in chick growth. Liley (1999) showed that ringed plover chicks spent less time foraging on disturbed sites but that this did not effect chick growth, suggesting that chicks on disturbed sites can compensate for any lost feeding time and this does not result in longer term consequences to survival. Yalden and Yalden (1990) showed that chick growth and survival was reduced on disturbed sites where chicks have less brooding by the adults and are likely to be exposed to inclement weather. Weather conditions are not included in these analyses but it is possible that stone curlew chick growth on disturbed sites could also be affected in this way. However, chick growth was not related to chick survival to fledging. Therefore it is considered that differences in growth rate may have minor consequences to overall survival and effects of weather and availability of food are greater influences.

Stone curlews further from A roads were likely to breed later, which is opposite to the relationship that may have been expected, but there were no other effects of disturbance on the timing of first breeding attempts (compare results in Chapter 8). There was also a difference in first egg date between years which is likely to be related to arrival date and weather conditions.

There was no evidence that disturbance reduces the probability of re-nesting following failures at the egg stage. Furthermore, whilst some studies have shown a direct impact of disturbance on

recruitment (e.g. Fernandez-Juricic and Telleria, 1990), this could not be adequately assessed due to the short period of study.

There is little evidence from this study to suggest that human disturbance is negatively impacting breeding success in this population of stone curlews, given that the pairs have settled to breed. Instead, nest and chick success appear to be driven by qualities of the individual birds, habitat type and predator activity. However, as observed in Chapter 6, stone curlews in this study population are already selecting the least disturbed plots to breed and so disturbance levels in the breeding population are low and do not vary greatly between sites. As a result, and similarly to a study on Malaysian plovers *Charadrius peronii* (Yasue and Dearden, 2006), if there is an effect of human disturbance on stone curlew breeding success, there is probably not enough variation in disturbance levels within the study area to detect it.

At present there may be sufficient potential nesting sites relative to breeding pairs of stone curlews for pairs to select sites of high habitat quality and low disturbance. However, as the stone curlew population grows and habitat becomes more limited (assuming the provision of nesting plots does not increase at the same rate), stone curlews may eventually be forced to breed on disturbed plots and it may be that their reproductive performance will suffer as a result.

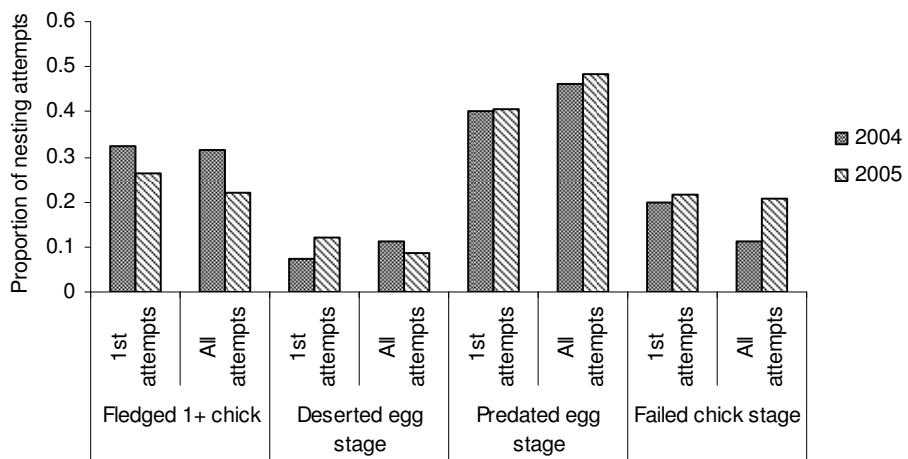


Figure 7.1. Fate of first nesting attempts and all nesting attempts in 2004 and 2005.

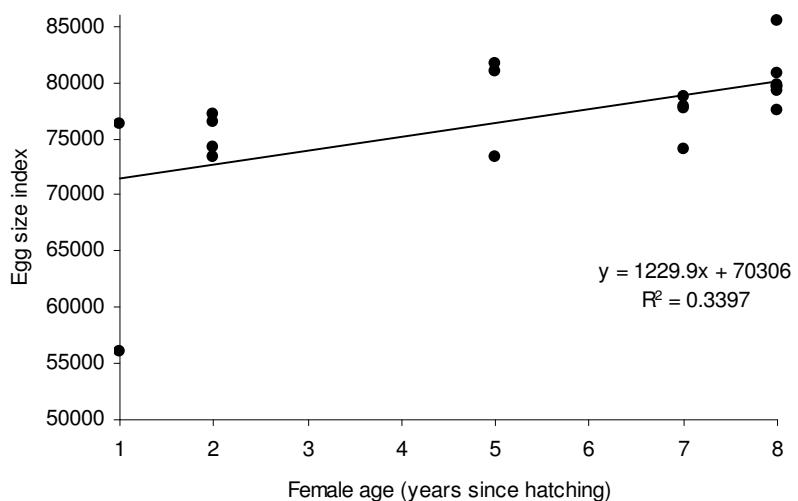


Figure 7.2. The relationship between mean nest egg size for two egg nests and female age. Points represent individual nests and the line is the linear regression.

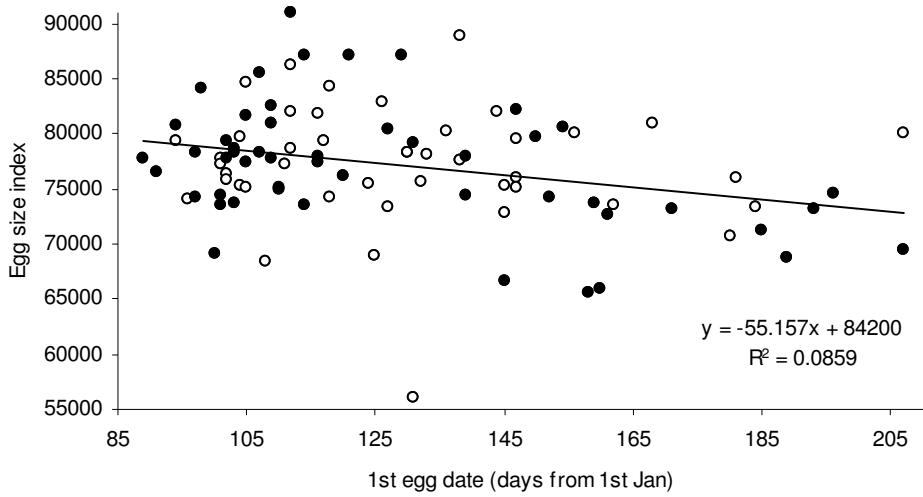


Figure 7.3. The relationship between egg size and 1st egg date. Points represent individual nests and the line is the linear regression. Open circles are data from 2004, closed circles are data from 2005.

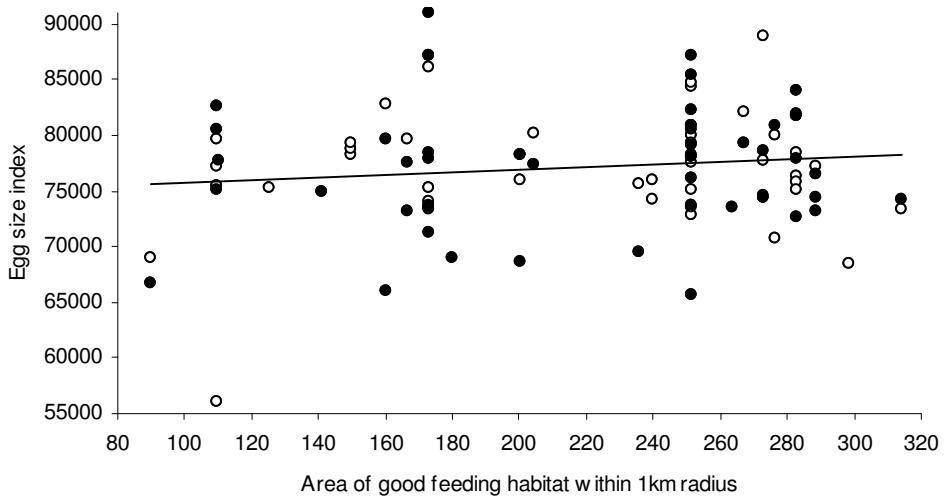


Figure 7.4. The relationship between egg size and the area of feeding habitat within 1km radius. Points represent individual nests and the line is the linear regression. Open circles are data from 2004, closed circles are data from 2005.

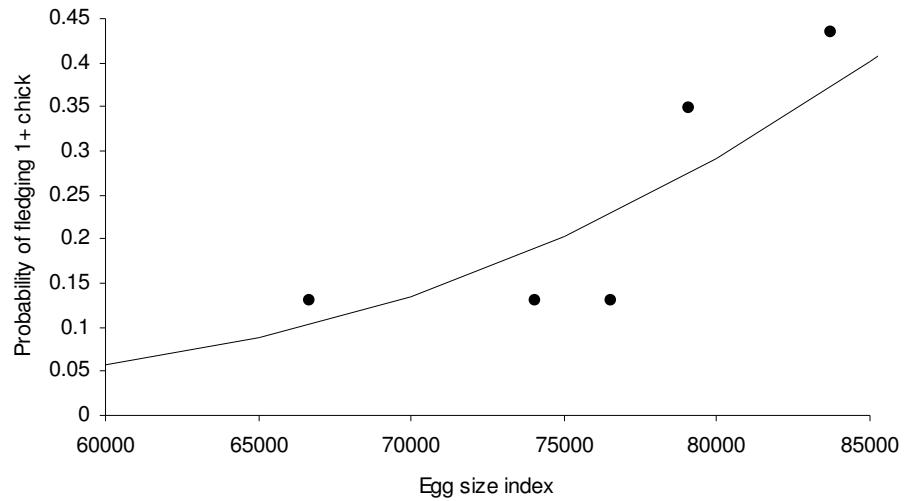


Figure 7.5. The relationship between probability of fledging one or more chicks and the egg size index. The points are for the proportion of nests fledging one or more chicks plotted in egg size bins and the line is the fitted logistic regression model.

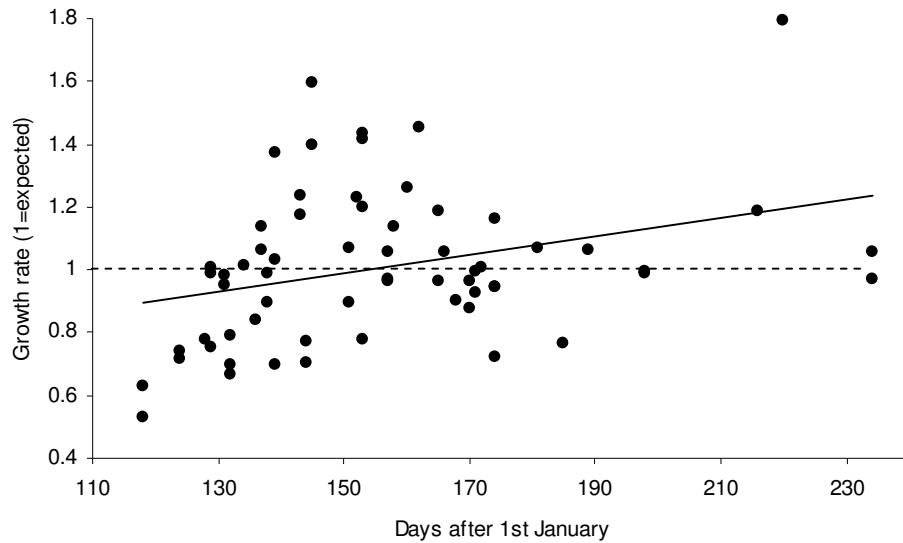


Figure 7.6. The relationship between chick growth rate index and hatch date. The horizontal line through one represents the average growth rate index for chicks that survived to fledging from the study of Day (2003). Points are for individual chicks and the line is the linear regression of growth rate index on hatch date. Points below the dotted line are chicks with an observed growth rate lower than that expected at the age they were measured. Points above the dotted line are chicks with a higher observed growth rate. Chicks hatched before the end of May grew slower than those hatched later in the season.

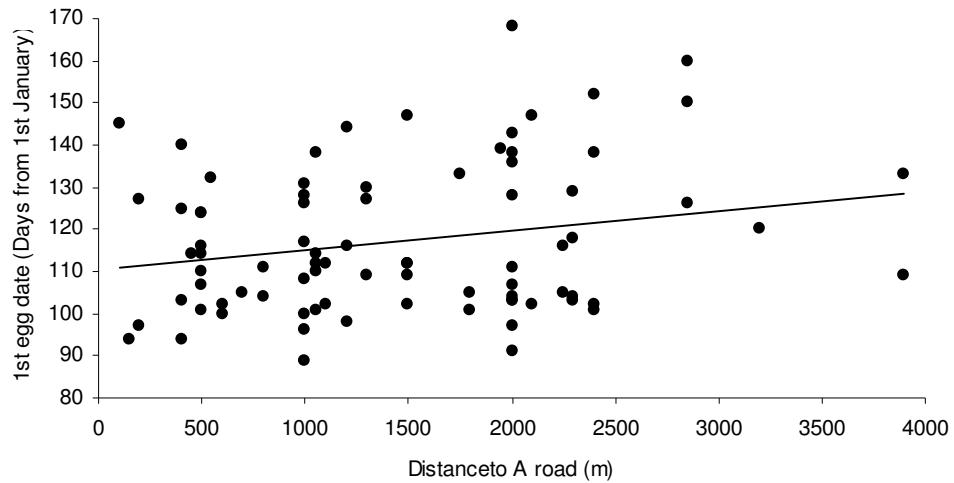


Figure 7.7. The relationship between first egg date of first clutches and distance to the nearest A road. Points represent individual nests and the line is the linear regression.

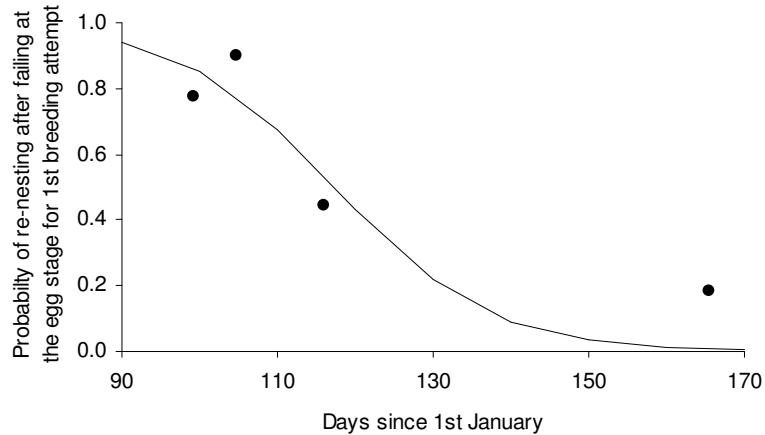


Figure 7.8. The relationship between probability of re-nesting after a failed first nesting attempt at the egg stage, and first egg date of the first breeding attempt. The points are for the proportion of stone curlews re-nesting after failing at the egg stage for 1st nesting attempts plotted in date bins and the line is the fitted logistic regression model.

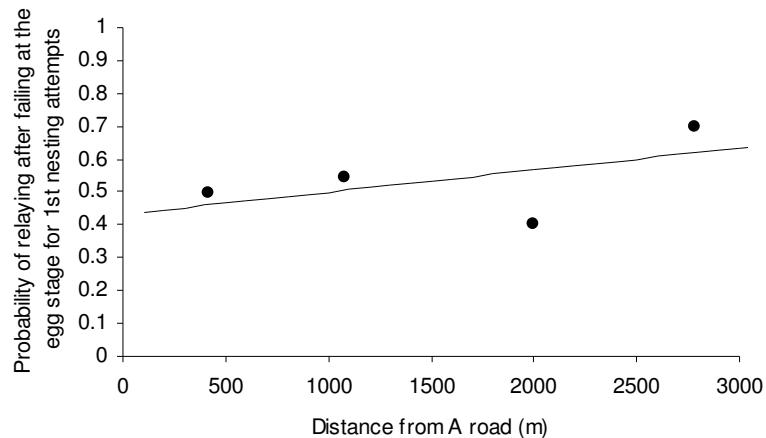


Figure 7.9. The relationship between probability of re-nesting after 1st nesting attempt egg stage failures, and distance to A road. The points are for the proportion of stone curlews re-nesting after failing at the egg stage for 1st nesting attempts plotted in distance bins and the line is the fitted logistic regression model.

Table 7.2. Results of multiple linear regression of egg size on female age for first breeding attempts using the reduced dataset where female age was known (n=20). The minimal adequate model is shown in bold with the parameter estimates and standard errors. For the variables in the minimal adequate model, F tests of their deletion from the MAM and the associated p values are given. For the remaining candidate variables, F tests and p values are given for the effect of adding the terms back into the minimal adequate model.

	Slope	Std. error	F	df	p
Intercept	70306.31	2453.38			
Female age	1229.93	404.15	9.261	1,18	0.007
Year		3.940	1,17	0.064	
1st egg date		3.721	1,17	0.071	
Area of suitable feeding habitat		2.591	1,17	0.126	
Settlement disturbance event rate		0.146	1,17	0.706	
Active responses per hour during settlement		0.477	1,17	0.499	
Season disturbance event rate		1.398	1,17	0.253	
Active responses per hour during season		3.235	1,17	0.090	
Distance to A road		0.141	1,17	0.712	

Table 7.3. Results of multiple linear regression of egg size on female age, year, first egg date and habitat quality for all breeding attempts, using the reduced dataset where female age was known (n=29). The minimal adequate model is shown in bold with the parameter estimates and standard errors. For the variables in the minimal adequate model, F tests of their deletion from the MAM and the associated p values are given. For the remaining candidate variables, F tests and p values are given for the effect of adding the terms back into the minimal adequate model.

	Slope	Std. error	F	df	p
Intercept	69621.01	4252.39			
Female age	1203.77	256.50	22.023	1,28	0.00006
1st egg date	-62.27	19.20	10.520	1,28	0.0030
Area of suitable feeding habitat within 1km	33.59	11.42	8.648	1,28	0.0065
Year		1.280	1,27	0.268	
Settlement disturbance event rate		0.706	1,27	0.408	
Active responses per hour during settlement		0.222	1,27	0.641	
Season disturbance event rate		0.079	1,27	0.781	
Active responses per hour during season		0.1192	1,27	0.733	
Distance to A road		1.190	1,27	0.285	

Table 7.4. Results of multiple linear regression of egg size on first egg date for first breeding attempts using the full dataset. The minimal adequate model is shown in bold with the parameter estimates and standard errors. For the variables in the minimal adequate model, F tests of their deletion from the MAM and the associated p values are given. For the remaining candidate variables, F tests and p values are given for the effect of adding the terms back into the minimal adequate model.

	Slope	Std. error	F	df	p
Intercept	84200.05	2469.74			
1st egg date	-55.16	18.76	8.645	1,92	0.0042
Area of feeding habitat with 1km radius		1.741	1,91	0.190	
Year		0.083	1,91	0.774	
Settlement disturbance event rate		0.221	1,91	0.639	
Active responses per hour during settlement		0.114	1,91	0.736	
Season disturbance events rate		0.563	1,91	0.572	
Active responses per hour during season		0.105	1,91	0.746	
Distance to A road		0.095	1,91	0.759	

Table 7.5. Results of multiple logistic regression of daily nest survival on potential explanatory variables for first nesting attempts. Parameter estimates of the variables in the minimal adequate model are given and the change in deviance and associated p value of their individual removal from the MAM. For the remaining terms in the starting model, the change in deviance and the associated p values are given of as a result of adding these variables into the MAM.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	4.577558			
Grassland habitat	-1.106324	8.66	1	0.0032
Corvid index		1.75	1	0.18
Year		0.18	1	0.66
1 st egg date		0.16	1	0.68
Distance to A road		0.5	1	0.44
Plot aspect		0.92	3	0.81
Distance to woodland edge		0.00046	1	0.98
Settlement disturbance event rate		2.61	1	0.10
Active response per hour during settlement		0.014	1	0.90
Season disturbance event rate		1.75	1	0.41
Active responses per hour during season		0.52	1	0.46
Rabbit index		0.016	1	0.89

Table 7.6. Results of multiple logistic regression of daily nest survival on potential explanatory variables for all breeding attempts. Parameter estimates of the variables in the minimal adequate model are given and the change in deviance and associated p value of their individual removal from the MAM. For the remaining terms in the starting model, the change in deviance and the associated p values are given of as a result of adding these variables into the MAM.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	4.98419			
Grassland habitat	-0.9388	9.16	1	0.0024
Corvid index	-0.1161	4.72	1	0.029
Year		0.0015	1	0.96
1 st egg date		0.10	1	0.75
Distance to A road		0.028	1	0.86
Plot aspect		0.77	3	0.85
Distance to woodland edge		0.060	1	0.80
Settlement disturbance event rate		2.23	1	0.13
Active response per hour during settlement		0.27	1	0.60
Season disturbance event rate		3.69	1	0.29
Active responses per hour during season		0.11	1	0.73
Rabbit index		0.12	1	0.78

Table 7.7. Results of multiple logistic regression of desertion with potential explanatory variables. Parameter estimates of the variables in the minimal adequate model are given and the change in deviance and associated p value of their individual removal from the MAM. For the remaining terms in the starting model, the change in deviance and the associated p values are given of as a result of adding these variables into the MAM.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	-1.8415			
Number of eggs laid	-0.6784	4.06	1	0.043
Egg size		0.052	1	0.819
Year		0.13	1	0.71
1 st egg date		0.24	1	0.61
Settlement disturbance event rate		0.049	1	0.82
Active response per hour during settlement		0.45	1	0.50
Season disturbance event rate		0.21	1	0.89
Active responses per hour during season		0.49	1	0.48

Table 7.8. Results of multiple logistic regression of probability of fledging on potential explanatory variables. Parameter estimates of the variables in the minimal adequate model are given and the change in deviance and associated p value of their individual removal from the MAM. For the remaining terms in the starting model, the change in deviance and the associated p values are given of as a result of adding these variables into the MAM.

	Parameter estimate	Reduction in residual deviance	df	p
Intercept	-8.5158			
Egg size	0.000105	19.90	1	0.010
Grassland habitat	-1.0724	4.89	1	0.026
Hatch date		1.08	1	0.29
Year		3.21	1	0.07
Area of plot		0.03	1	0.86
Area of feeding habitat within 1km radius		0.44	1	0.50
Plot aspect		0.78	3	0.85
Distance to woodland edge		2.38	1	0.12
Distance to A road		0.01	1	0.88
Settlement disturbance event rate		0.34	1	0.55
Active responses per hour during settlement		0.087	1	0.76
Season disturbance event rate		0.36	1	0.83
Active responses per hour during season		0.14	1	0.70
Corvid index		0.02	1	0.88

Table 7.9. Results of multiple linear regression of chick growth rate index on potential explanatory variables. The minimal adequate model is shown in bold with the parameter estimates and standard errors. For the variables in the minimal adequate model, F tests of their deletion from the MAM and the associated p values are given. For the remaining candidate variables, F tests and p values are given for the effect of adding the terms back into the minimal adequate model.

	Slope	Std. error	F	df	p
Intercept	0.5486	0.1537			
Hatch date	0.0034	0.0010	10.79	2,58	0.00010
Year	-0.4811	0.1517	6.60	2,58	0.0025
Disturbed plot	-0.1114	0.0297	14.11	1,58	0.00040
Year*hatch date	0.0027	0.0010	8.02	1,58	0.0063
Chick type		1.45	2,56	0.24	
Grassland habitat		2.0	1,58	0.16	
Egg size		0.46	1,46	0.49	
Area of feeding habitat in 1km radius		0.19	5,57	0.65	

Table 7.10. Results of multiple linear regression of the first egg data of first breeding attempts on potential explanatory variables. The minimal adequate model is shown in bold with the parameter estimates and standard errors. For the variables in the minimal adequate model, F tests of their deletion from the MAM and the associated p values are given. For the remaining candidate variables, F tests and p values are given for the effect of adding the terms back into the minimal adequate model.

	Slope	Std. error	F	df	p
Intercept	110.3544	3.5667			
Distance to A road	0.0047	0.0021	10.05	1, 79	0.0021
Year	-5.6993	1.7972	4.96	1,79	0.028
Age		0.78	1,26	0.38	
Settlement disturbance event rate		0.00049	1,78	0.98	
Active response per hour during settlement		0.53	1,78	0.46	
Season disturbance event rate		0.0073	1,78	0.93	
Active responses per hour during season		0.28	1,78	0.59	

Table 7.11. Results of multiple logistic regression of probability of a clutch lost at the egg stage being replaced on potential explanatory variables. Parameter estimates of the variables in the minimal adequate model are given and the change in deviance and associated p value of their individual removal from the MAM. For the remaining terms in the starting model, the change in deviance and the associated p values are given of as a result of adding these variables into the MAM.

	Parameter estimates	Reduction in residual deviance	df	p
Intercept	12.72208			
1st egg date	-0.12111	21.53	1	0.0000035
Distance to A road	0.00098	4.54	1	0.032
Days between first egg date and failure for failed clutch		1.30	1	0.25
Area of feeding habitat in 1km radius		1.18	1	0.27
Settlement disturbance event rate		0.61	1	0.43
Active response per hour during settlement		3.65	1	0.055
Season disturbance event rate		0.18	1	0.66
Active responses per hour during season		0.60	1	0.43
Year		2.01	1	0.069

8 Movements of stone curlew pairs between sites before they settled to breed

8.1 Summary

Although relatively faithful to breeding sites between years, observations of colour ringed adults before the breeding season revealed that 40% of stone curlew pairs arriving in spring move between sites before settling to breed. Pairs were likely to move if disturbance at the first potential breeding site they visited was high during settlement. Furthermore, for pairs that moved, the second site chosen was significantly less disturbed than the first site. Although no clear effect on breeding success was found, pairs that moved sites bred one week later than those that did not move. This is likely to reduce the chance of producing two broods and of laying replacement clutches after failure.

8.2 Introduction

Previous work has shown that stone curlew behaviour is sensitive to disturbance (Chapters 3, 4 and 5). Birds react at long distances and both the frequency of disturbance and frequency of expected behavioural responses can be used to predict the probability of a nesting plot being used for a breeding attempt (Chapter 6). Although mostly faithful to breeding sites between years (Green, 1995), colour ringed stone curlews often breed in different sites between and within seasons in Wessex. Of the 13 colour ringed individuals three years and older which have been known to breed at least three times since 1999 in my study area, Figure 8.1 shows the number of sites used in all known breeding years (when the same site was available in all known breeding years). Only 10% used the same site for all of their known breeding attempts.

In Chapter 6 I showed that sites were avoided for breeding if disturbance event rates and expected rates of active responses were high. Therefore I considered the possibility that stone curlew pairs may settle on sites with suitable habitat early in the season but move to less disturbed sites to breed if disturbance exceeds a threshold during settlement. Alternatively, stone curlews pairs may only return to sites with relatively low disturbance levels and remain to breed whatever the disturbance levels they then experience. The high proportions of colour ringed individuals in the population make it possible to test this hypothesis.

8.3 Aims of chapter

The aim of this chapter is to address the following questions:

1. Do individually marked birds move between potential breeding sites in spring?
2. What proportion of stone curlew pairs move between sites with suitable habitat before settling to breed?
3. What determines whether pairs move?
4. How do the first and second choice sites differ?
5. Does movement before settlement have consequences for breeding performance?

8.4 Methods

8.4.1 Defining a settlement period

I defined a settlement period as being 20 March – 20 April. Figure 8.2 shows the cumulative proportion of pairs arriving on first choice sites in relation to date and the cumulative proportion of first egg dates. Arrival dates and first egg dates in 2004 and 2005 were combined and the mean proportion calculated. Approximately 10% of birds had arrived by 20th March, with 65% back by the end of the settlement period; and approximately 50% of pairs had their first egg date by 20 April.

8.4.2 Data collection

Site selection, stone curlew watching and disturbance surveys followed methods described in sections 2.4.1, 2.4.2 and 2.4.3. Disturbance rates were calculated using the method in section 2.5.2 and the expected number of active responses was calculated using the protocol in Chapter 5. Habitat, predator surveys, rabbit surveys and landscape measurements are described in Chapter 6, sections 6.4.1, 6.4.2, 6.4.3 and 6.4.4 respectively. Unlike Chapter 6, specific measurements of vegetation cover and heights at the nest and intermediate scale were used in these analyses as well as the compound vegetation variables. Additional variables measured and used as explanatory variables in this chapter are shown in Table 8.1.

8.5 Data Analysis

For analyses in this chapter, disturbance was represented as settlement disturbance event rate. Additionally, disturbance was expressed as the expected number of active responses per hour during settlement based on the behaviour predicted by the models in Chapter 4 and the methods in Chapter 5.

Data from 2004 and 2005 were analysed together. The data were not normally distributed so I used non-parametric univariate tests to test differences for several variables (Table 8.2) between pairs that moved site and those that did not. I then fitted binomial logistic regression models with movement or not as the binary dependent variable and the measured attributes of pairs and sites as explanatory variables (Table 8.2). I selected minimal adequate models (MAMs) of the probability of a movement occurring during settlement. The performance of minimal adequate models in successfully classifying pairs as having moved or not during settlement was assessed using receiver operating characteristic (ROC) curves (Osborne *et al.*, 2001), as described in Chapter 5.

Differences in attributes (Table 8.2) between the first and second choice sites were tested using non-parametric paired tests. There was not enough variation between categories to compare the attributes of first and second choice plots in a meaningful way for factor variables.

Daily nest survival rates were calculated following Mayfield's method (Mayfield, 1975) for nests where outcomes were known.

8.6 Results

8.6.1 Evidence of birds moving before settlement

There are historical accounts of spring assemblies of stone curlews similar to autumn roosts on sites that do not become breeding sites (Walpole-Bond, 1938, Ogilvie, 1920). It is therefore, suggested that some plots may act as staging areas for spring assemblies from which pairs relocate mates or acquire mates and disperse to breeding sites. Alternatively spring assemblies may comprise non-breeding or young birds which are unable to secure territories at other sites. In both 2004 and 2005 two plots hosted multiple (5-8) birds for 7-10 days very early in the season (E. Taylor pers. obs.). Birds at these assemblies were not included in this analysis as it was not clear what was happening at these sites and the majority of individuals were unringed.

In two years of data collection, 67 pairs of stone curlews arrived on first choice nesting sites in Wessex before 21 April, but almost 40% of these were observed to move to another site before breeding (Table 8.3). 53 of these pairs included one or more individually colour ringed bird. Of the remaining 14 pairs, seven remained on the first choice site (where it was assumed that this was the original pair) and seven moved sites. Of the seven un-ringed pairs that moved, three were distinguishable by having foot or leg injuries. For the remaining four un-ringed pairs, birds

disappeared from one site and another un-ringed pair appeared on the next nearest available plot within 3 days so it was assumed these pairs were the same.

8.6.2 Differences between pairs that move and do not move

Was there a difference in habitat quality between sites where pairs moved and did not move?

There was no difference in any of the measured nest site habitat variables between pairs that moved and did not move (Table 8.4), except that the rabbit numbers at sites from which pairs moved away was significantly higher. Stone curlews were also significantly more likely to move sites if the first choice site had been used infrequently by any pair since 1999 (Table 8.5). There were no other measured habitat differences at the intermediate or landscape scale between pairs that moved and those that did not (Table 8.5).

Does experience influence movement?

Of the 39 pairs where a full colour ring combination of at least one bird was known, there was no difference in mean age (Mann Whitney U=129.5, df=38, p=0.442), maximum age (the age of the older bird in the pair) (Mann Whitney U=134.5, df=38, p=0.540) or minimum age (the age of the younger bird in the pair) (Mann Whitney U=125.5, df=38, p=0.370) between pairs that moved site and those that did not. There was also no difference in the number of years since confirmed first breeding between pairs that moved and did not move (Mann Whitney U=26.0, df=20, p=0.275).

There was no evidence of pairs arriving later being more or less likely to move (Mann Whitney U=519.5, df=66, p=0.862) and arrival date was not correlated with age for mean pair age ($r=0.131$, $n=39$, $p=0.426$), maximum age ($r=0.125$, $n=39$, $p=0.449$) or minimum age ($r=0.136$, $n=39$, $p=0.409$). There were also no correlations between pair age ($r=-0.202$, $n=39$, $p=0.217$), maximum age ($r=-0.201$, $n=39$, $p=0.217$), or minimum age ($r=-0.201$, $n=39$, $p=0.217$) and start of breeding (first egg date).

Pairs were significantly more likely to move plots if they had not used the site in the previous year (only pairs two years old or older and sites that were available in the previous year were included here) (Fisher's Exact test $p=0.0039$) and if they had not used the site very frequently since 1999 (Mann Whitney U=270.0, df=66, $p=0.001$).

Was there any difference in relative predator abundance between sites where birds moved and did not move?

The only predator information that was suitable for analysis was the mean maximum number of corvids observed using the site per 1-hour watch throughout the season. This variable was not different between sites where birds moved and did not move (Mann Whitney U=495.0, df=66, p=0.624).

Did birds on more disturbed sites move?

Pairs that moved sites during settlement were likely to be on more disturbed plots (Figures 8.3 and 8.4).

8.6.3 Multiple regression models of the probability of moving plots during settlement

I used binomial logistic regression to test whether the variables that emerged as having a significant effect in univariate tests predicted the probability of movement during the settlement period. The MAMs describing the probability of moving in relation to explanatory variables are shown in Tables 8.6 and 8.7. Separate MAMs were selected with each of the two disturbance variables as candidates. Both MAMs include the disturbance variable and the recent use by any pair (Figure 8.5). Results for models containing just the disturbance variables are shown separately in Tables 8.8 and 8.9 and Figures 8.6 and 8.7. Model performance is assessed in Figures 8.8 and 8.9 and Table 8.10.

Settlement disturbance event rate is a slightly better predictor of movement than the expected number of active responses per hour (Tables 8.8 and 8.9) in terms of significance of the terms in the models. However, the ROC curves show that the models using the expected number of active responses per hour classify the data better (Figures 8.8 and 8.9 and Table 8.10). Additionally, the settlement disturbance event rate is highly correlated with several other variables (Table 8.11). This is a result of many plots being on SPTA where there is frequent disturbance (mostly vehicles), away from roads and in good habitat.

8.7 What were the differences between the first and second choice site for pairs that moved during settlement?

The mean distance moved between sites during settlement was 1523.56m (SD 364.25), although an extreme distance of 8970m was recorded. The second choice sites were significantly further

away from other occupied plots (Table 8.12) and less disturbed in terms of disturbance events per hour (Figure 8.10) and the expected number of active response per hour (Figure 8.11). The second choice site was also significantly different in terms of how much additional breeding habitat there was with 1km radius (Table 8.12)

Of the birds that moved, only two of sixteen pairs (birds that bred in previous year and full colour ringed combinations known) returned to the site they had used for breeding in the previous year. Furthermore, there was no indication of pairs moving to sites they had used regularly since they first began to breed (Table 8.12). Other features were not different between the first and second choice of sites (Table 8.12).

8.8 Competition

Of the 23 pairs that moved sites during settlement (excluding the DTA where space is not limited), five of the first choice plots were used for nesting by another pair of stone curlews after the first pair had left. Of these five, one was occupied by a pair that had used the site previously, possibly indicating competition for that plot. The mean time between one pair leaving a plot and another pair arriving was 10.60 days (SD 15.34). This suggests that movement from one site is independent of the replacement pair's arrival. One of the five plots was occupied by two pairs simultaneously for approximately four days before the first pair moved to a neighbouring plot. This was one of the few instances of birds moving onto a *more* disturbed site and competitive displacement or avoidance might be the cause. There is not enough colour ring information to know whether the pairs moving onto rejected plots were young or old birds.

Six out of 26 pairs that moved plots used the first choice site later in the breeding season for a subsequent nesting attempt where nest scale habitat on the second choice plot became unsuitable for breeding.

8.9 What are the consequences for breeding performance of moving sites during settlement?

The mean time between arrival and first egg date for all pairs was 21.9 days (SD 14.3). Stone curlews that moved plots during settlement had significantly longer delays between arrival date and first egg date (Figure 8.12). Those that did not move started breeding at 18.9 days (SD 13.6) after arrival, whilst those that moved did not breed until 27.2 days (SD 14.1) after arrival. However, time from arrival to breeding was negatively correlated with arrival date so that birds

that arrive later breed sooner after arrival ($r=-0.321$, $n=65$, $p=0.009$). Two pairs in 2004 that moved plots during settlement were not confirmed to breed anywhere. Full colour ring combinations were not obtained for these birds so their exact age is unknown and the possibility that they were young non-breeders can not be excluded.

There was no correlation between time between arrival and breeding and either disturbance events per hour during settlement ($r=0.050$, $n=65$, $p=0.169$) or the expected number of active responses per hour during settlement ($r=-0.173$, $n=65$, $p=0.169$).

There was no evidence that movement during settlement had any direct impact on breeding success. There was not a significant difference in first nest Mayfield daily nest survival probability for the incubation period between pairs that moved and did not move (Table 8.13). The proportion of pairs successfully fledging one or more chicks was also not significantly different ($\chi^2=0.58$, $df=1$, $p=0.45$), and there was no difference in the number of confirmed fledged chicks per pair and per season between pairs that moved and did not move (Table 8.13). There was also no difference in the proportion of hatched chicks surviving to fledging between those that moved and those that did not ($\chi^2=0.10$, $df=1$, $p=0.75$).

8.7 Discussion

Over two years of data collection, almost 40% of stone curlew pairs moved from the plot where they were first observed before settling to breed on another plot, suggesting that the first choice plot was unsuitable in some respect for breeding. This is not the first study to report movements of stone curlews from sites before settling to breed. There are historical accounts of stone curlews visiting sites in spring but not subsequently using them for breeding (Pettit, 1915). However, these accounts did not follow individually marked adults and so could not observe differences between sites and establish reasons for movements.

Selection of breeding habitat is a vital decision for birds as it can not only affect the success of a breeding season, but a poor choice may negatively affect the long term reproductive success of an individual (Thomson *et al.*, 2006). It is widely accepted that, over evolutionary time, natural selection has shaped nest-site preference so as to minimise the risk of predation (Newton, 1998, Roos and Part, 2004) whilst optimising food availability, thus resulting in a trade-off between the two (Gotmark *et al.*, 1995). As a result, it is well known that birds respond to the risk of

predation in such a way to avoid being killed (Lima and Dill, 1990) or to avoid predation of eggs and chicks, and many species avoid nesting close to potential predators (e,g, Meese and Fuller, 1989, Forsman *et al.*, 2001). However, few studies have addressed the question of whether birds are capable of directly assessing variation in risk which means they then go on to choose the least risky nest site (Forstmeier and Weiss, 2004). This is known as *adaptive plasticity* in nest site section (Forstmeier and Weiss, 2004). In order to make such choices, individuals need to gather information on potential breeding sites in order to make optimal decisions when selecting a nest site (Wiens, 1976, Doligiez, Part and Danchin, 2003). It is thought the information gathered makes it possible for decision-making to be flexible and control for unpredictability in the environment (Stamps, 2001, Thomson *et al.*, 2006).

Most studies that demonstrate breeding birds showing adaptive plasticity when choosing nests sites, show that birds use so called ‘public information’ to monitor the reproductive success of conspecifics to assess habitat quality and then use this information to select their own nest sites (Doligiez, Danchin and Clobert, 2002) *in the following year*. For example, it is thought that male collared flycatchers *Ficedula albicollis* ‘prospect’ conspecifics’ nests at the peak of the breeding season and use information on reproductive success to help in patch selection in the next breeding season (Doligiez, Part and Danchin, 2004). This ‘public information’ may provide a reliable indication of overall environmental quality (Thomson *et al.*, 2006), because the reproductive output of conspecifics will depend on factors such as feeding quality, predation levels and inter- and intra- specific competition. However, as Thomson *et al.* (2006) suggest, this measure of habitat quality may be outdated in the next year and so it would benefit species *more* if they were able to use information *prior* to habitat selection and reproductive investment.

There is, however, growing evidence that birds *are* able to track changes in patch quality *before breeding* to make optimal decisions concerning nest site choice in that year (Badyaev *et al.*, 1996, Petit and Petit, 1996, Forstmeier and Weiss, 2004). For example, dusky warblers *Phylloscopus fuscatus* have been shown to have the ability to use information on predator abundance in territories to select the safest nest site. In years with high Siberian chipmunk *Tamias sibiricus* density, warblers chose nests sites based on potential predation risk rather than microclimate or food factors, and selected nest sites significantly higher off the ground than in years with a lower predator population (Forstmeier and Weiss, 2004).

As it is thought that birds may react to human disturbance in a similar way to predators, it is suggested that high levels of disturbance may lead to subsequent avoidance of certain sites for breeding (Frid and Dill, 2002). As far as I have found, however, there have been no studies which use the adaptive plasticity hypothesis and show that birds can make assessments of breeding sites *in terms of human disturbance* before settlement and then use this information to select less disturbed sites to breed. In this study, stone curlews on more disturbed sites were significantly more likely to move to another site before settling to breed. Both the disturbance event rate during settlement and the expected number of active responses per hour during settlement were predictors of movements and for both variables the apparent tolerance thresholds were extremely low.

In the case of the stone curlew, there is so far little evidence of a relationship between reproductive output and disturbance (Chapter 7), (although as shown in Chapter 6, pairs avoid nesting in the most disturbed areas so disturbance levels on breeding sites are low and do not vary much), but nevertheless, highly disturbed sites are avoided. Therefore, adult stone curlews must associate disturbed sites with high risk either to themselves or their nests. Unnecessary avoidance of areas of high predation risk has been observed in pied flycatchers *Ficedula hypoleuca* nesting in nest-boxes, even though the actual predation rate for nest-box birds was extremely low (less than 1.5%) (Thomson *et al.*, 2006). It is suggested that flycatchers evolved with high predation rates in tree cavities. They therefore evolved predator avoidance during nest site selection and have not had time to evolve tolerance of predators when breeding in modern nestboxes. Alternatively, the authors also suggest that flycatchers are avoiding the high risk areas because they actually do not know what the risk is and so they are ensure predictability by selecting nest boxes away from risks, rather than the unpredictable outcome of nesting close to predators (Sergio *et al.*, 2003). It is possible that stone curlews are showing the same response. By gathering information on disturbance levels at plots prior to settling, stone curlews are able to make decisions on whether to make a reproductive investment at that site. Movements of birds away from disturbed areas may then be a result of using past experience of negative effects of breeding in disturbed areas, or more likely given the results from Chapter 7, they are hedging their bets and avoiding disturbance because they do not know the consequences of remaining on disturbed sites.

Observations and movements of specific pairs or birds is only possible where they are individually colour marked and can be identified without re-capture, or by radio tracking

therefore few other studies have been able to follow individual animals and determine the effects of disturbance on habitat choice. In fact, I found no other studies of movements of individually marked birds between potential breeding sites in response to disturbance. There are, however, a number of studies of other individually marked taxa apparently tracking changes in disturbance levels and changing their distribution in response, although these are mostly not in the breeding season and can not really be described as examples of adaptive plasticity of habitat choice. Lunn *et al.* (2004) deployed 19 satellite radio collars on adult female polar bears *Ursus maritimus* in Hudson Bay to study how pregnant females select maternity-den sites. Bears that had been subjected to disturbance through aircraft observations and capture, relocated to alternative denning sites large distances away from the first choice site. Undisturbed bears were significantly less likely to move and any that did move remained close to the original den. No effect of movement, however, was observed on breeding success. In this study disturbance around denning sites was not measured, rather bears themselves were classed as disturbed or not disturbed based on their past experience. Therefore whilst bears that had experience of being disturbed were more likely to move, it was not known how the second choice site differed in terms of actual disturbance. In another bear study, radio-collared grizzly bears *Ursus arctos* exposed to disturbance from the extraction industry, suffered a home range displacement which meant that the effective carrying capacity of the habitat for individuals was reduced (McLellan and Shakleton, 1988). Additionally, radio tagged Florida panthers *Puma concolor coryi* reduced their use of certain areas in their range during times when human pressure exceeded a threshold during the hunting season and were more likely to move to areas where human presence was lower (Janis and Clark, 2002). Conversely, a study of radio-collared black bears *Ursus americanus* showed that habitat use did not change in direct response to changes in military training (Telesco and Van Manen, 2006). Furthermore, whilst radio telemetry of rattlesnakes showed that disturbance caused reduced movement and sightings of individuals, snakes preferred to alter their behaviour and hunt at different times of the day rather than abandon heavily disturbed sites completely, even when alternative sites were available (Parent and Weatherhead, 2000). This is in contrast to Brown (1993) who observed abandonment of traditional ‘snake rocks’ by marked snakes in favour of alternative sites when disturbance threshold were exceeded.

In addition to disturbance there were other factors that were associated with movements in this study. Stone curlews were likely to move away from sites that had been infrequently used by any pair. This may be a measure of the attractiveness of the site and may be related to other factors, such as food availability. Although not significant, there was a negative correlation between

frequency of site use since created and mean disturbance levels across the study period. Therefore, it is possible that disturbance has been driving use of plots over a time period longer than that of this study but as retrospective disturbance levels are not known, this can not be properly tested. Stone curlews were also likely to move away from sites which the pair themselves had used infrequently since they were first observed to breed and if they had not used the site in the previous breeding season. Stone curlews are faithful to breeding sites to some extent and may settle temporarily on plots before moving to other sites they have experience of. However, there was no difference in the number of years pairs had used sites for breeding between the first and second choice sites and pairs did not seem to be returning to their most regularly used site. Additionally, only 13% of moving birds returned to the site they had used in the previous year. Therefore site faithfulness factors do not seem to be driving the movements of stone curlews between breeding sites. It is also thought that competition is unlikely to be a factor in determining movement off sites as only one plot was observed to be occupied by more than one pair at once. Furthermore, for those sites that were moved off by one pair but subsequently used for nesting by another pair, there was a long time period between occupancies.

Predator abundance and nest site and intermediate scale habitat quality were not different between sites where birds moved and did not move. Corvids were the only potential predators to be recorded in this study and these are not thought to be the major predator of stone curlew eggs or chicks (refer to Chapter 7), therefore the perceived predation risk from corvids at a site may not be strong enough to cause a movement to another site. The negative relationship between movement and rabbit numbers at the nest site scale is likely to be spurious and a result of rabbits being correlated with another unmeasured variable. Stone curlews mostly forage at night, within 1 km of the nest site (Green et al., 2000). The same study also reports that individual stone curlews use a home range comprising on average 30 ha of suitable foraging sites. There were no differences in the availability of foraging habitat within 1 km radius between sites stone curlews moved from and sites where they remained. However, most sites in this study had in excess of 60 ha of suitable foraging sites within 1 km radius early in the season so lack of effect of this variable may be expected. Lack of apparent association between movements and variables such as habitat and roads is likely to be a product of site placement in the landscape. Effort is taken to place plots in areas where they are likely to be used (i.e. close to feeding habitat, away from roads etc), and whilst plots are not created in areas of very high disturbance, the assessment of disturbance by land managers is difficult (Chapter 2).

Lack of relationship between movement and distance to next unoccupied nesting plot suggests that birds do not avoid moving if there is nowhere to move to. Additionally, only 42% of those that moved went to the next nearest available plot, so they do not simply move because there is another plot nearby. There was also no suggestion that younger birds and those with less breeding experience were any more likely to move between plots.

For pairs that moved, the second choice site was less disturbed than the first in terms of both disturbance measures. This strengthens the argument that disturbance during settlement drives movement. If stone curlews moved from disturbed sites but selected alternative sites where disturbance levels were similar it is more likely that another factor would be driving the decision. Only one pair of stone curlews moved to a more disturbed site and in this case competitive displacement may have occurred because the birds were initially sharing a site with the pair that used the site in the previous year. There was also a suggestion that second choice sites had lower vegetation immediately off the site, which may be a sign of habitat quality being selected for. However, the first choice sites were not different in this respect and as discussed previously, for foraging, landscape scale habitat may be more important. Stone curlews were not more likely to move if they were closer to other pairs but the second choice site had less additional breeding habitat close by and was significantly further away from occupied sites. This could be a sign of stone curlews selecting sites where competition with other pairs is reduced or it could be just a product of site placement in the landscape. Stone curlew plots are usually at least 1km apart, even though in semi-natural habitats pairs may nest significantly closer (E.C. Taylor pers obs).

Some of the sites which stone curlews moved from did get used by the same pair later in the season for replacement nests or second broods. This apparent switch back to the inferior plot may be result of a change in disturbance levels between settlement and the whole season. Alternatively it may represent the second choice becoming unsuitable for breeding in terms of habitat or predation and a trade off being made between benefits and risks for the original plot for subsequent breeding attempts. It is also possible that stone curlews that were observed to move were actually prospecting early in the spring for alternative sites to use after first broods or failures.

Birds that moved to avoid disturbed sites did breed later but there was no difference in nest survival or the number of chicks fledged. Delayed breeding may be beneficial in some circumstances, for example if inclement weather conditions are avoided in early spring.

However, a delay in starting to breed means chicks hatch and fledge later, which could have survival consequences if peak food availability is mis-timed and it could also lead to a failure to produce replacement clutches or a second brood.

The two pairs that moved from their first choice site but were not observed to breed may not have found an alternative site; may have been young birds; or may bred outside of the study area. I am confident that they did not remain in my study area because suitable breeding habitat was fairly limited and coverage was good. They were also not observed by the Wessex stone curlew team on plots in the wider area. Therefore, if they did breed they must have gone far from the core of the population or bred in less secure habitat e.g. arable crops, where their presence went unnoticed. Unfortunately, the age of these two pairs is unknown because full colour ring combinations were not read in the field. Therefore the possibility that they were young birds and non-breeders cannot be excluded.

The ability to move sites to optimise the quality of breeding habitat does depend on the availability of alternative sites. At present, the Wessex stone curlew population is not habitat limited and a choice is available to stone curlews but as the population continues to recover, site availability may become limited. It is suggested that this could result in increased competition for breeding sites and consequences on breeding success may be observed.

There is likely to be a degree of individual variation and habituation in the tolerance of stone curlews pairs to disturbance. This is likely to be a trade off between threat and benefit of using a site. Although the settlement movement model predicts that few birds would remain on sites where the expected number of active responses during settlement exceeds two, there was an occupied site in the study where the disturbance level approached this figure. This site was optimal in terms of habitat, having the greatest amount of foraging habitat available nearby out of all the study sites and it is possible that disturbance is tolerated in order to benefit from good feeding.

Colour ringing and individual marking has many applications in conservation (e.g. Cormack 1964). This study illustrates the usefulness of individually colour ringed birds in a study population where the effects of disturbance are being examined. Without individual markings, observations of movements would not have been possible and the distribution of breeding pairs in

the landscape could only be examined once birds were settled to breed (Chapter 6). However, this study has shown that some of the sites that are avoided for breeding by stone curlews are actually examined by pairs in early spring but disturbance causes abandonment in favour of other sites. Adaptive plasticity in nest site choice has been observed in response to ‘public information’ gathering by birds and assessment of perceived predation risk but this is thought to be the first study of its kind following colour ringed birds during spring settlement and observing movements between potential breeding sites in response to human disturbance.

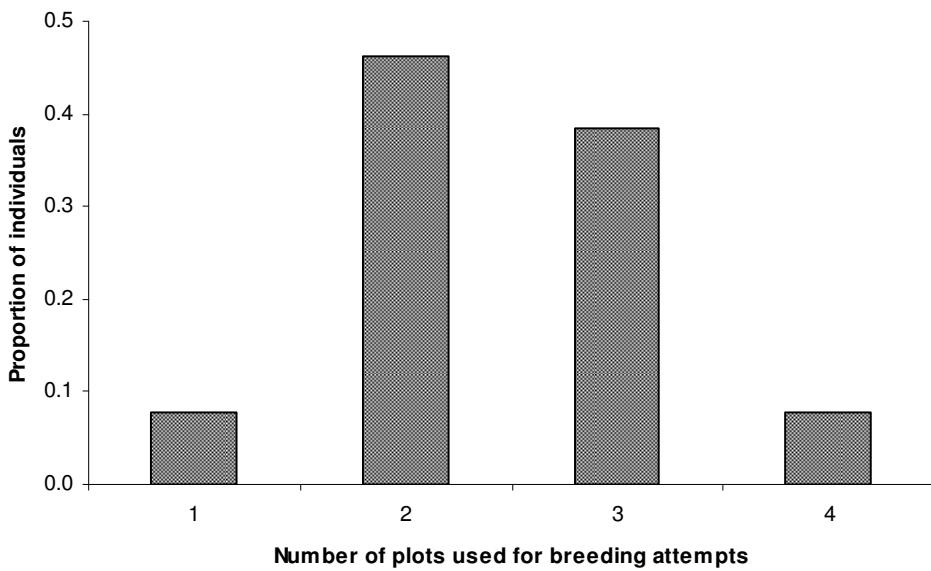


Figure 8.1. The number of plots used by individuals of age 3+ which have bred 3+ times since 1999.

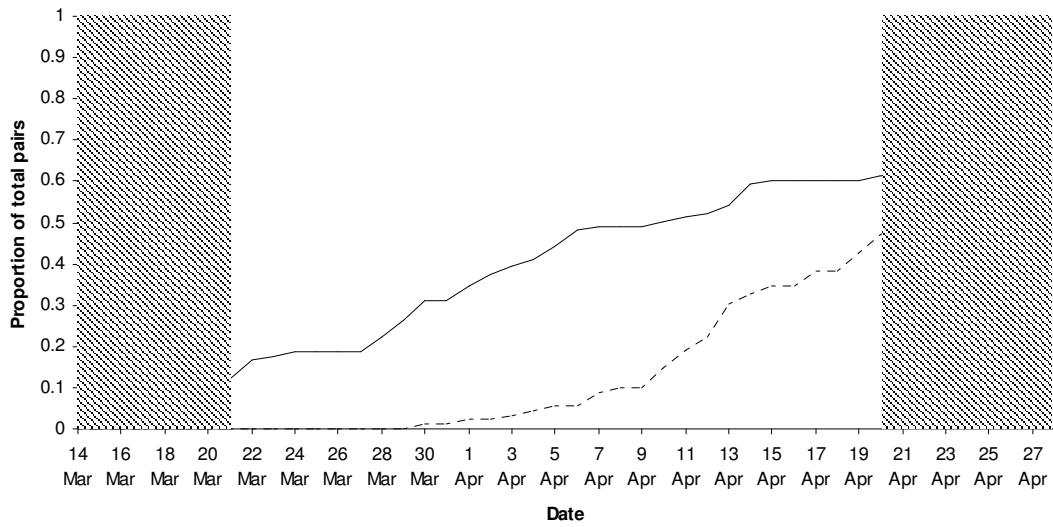


Figure 8.2. The cumulative proportion (mean of 2004 and 2005) of pairs of stone curlews arriving on first-choice nesting sites in spring in relation to date (black line) and the cumulative proportion of 1st egg dates (dotted line). Shading shows the boundaries of the settlement period.

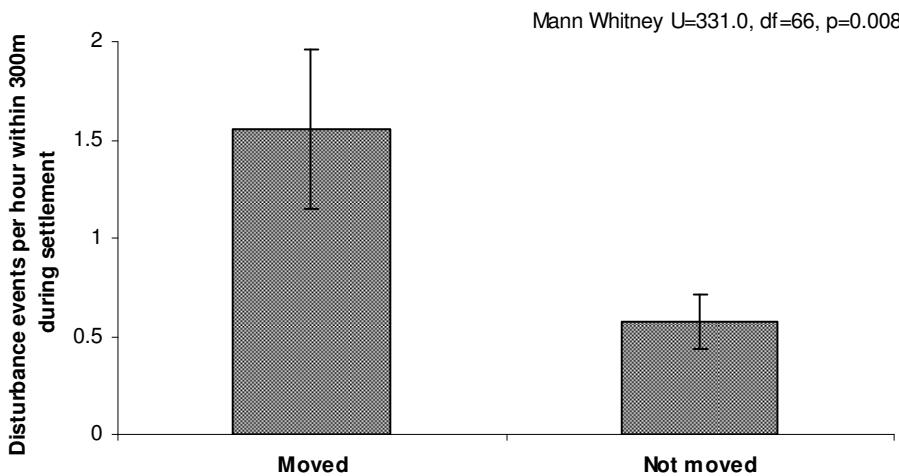


Figure 8.3. Stone curlews were significantly more likely to move sites if the first choice site was more disturbed.

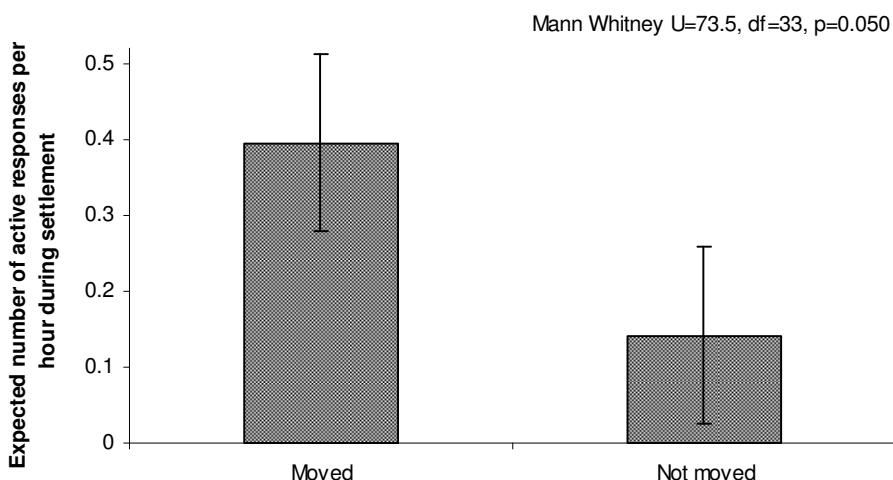


Figure 8.4. Stone curlews were significantly more likely to move in site where there was a higher number of expected active responses per hour

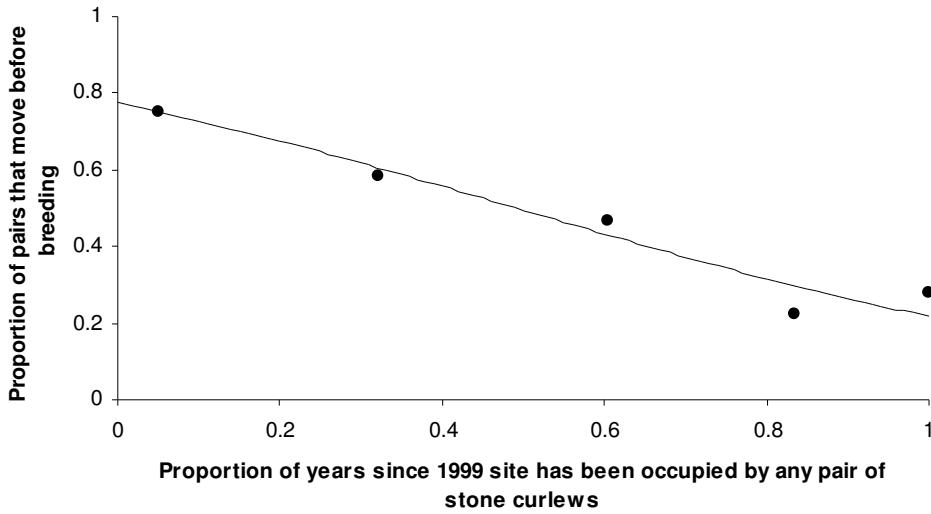


Figure 8.5. Logistic regression model fit (lines) and observed binned data (points) of the probability of a movement between sites during settlement in relation to the historic use by any pair.

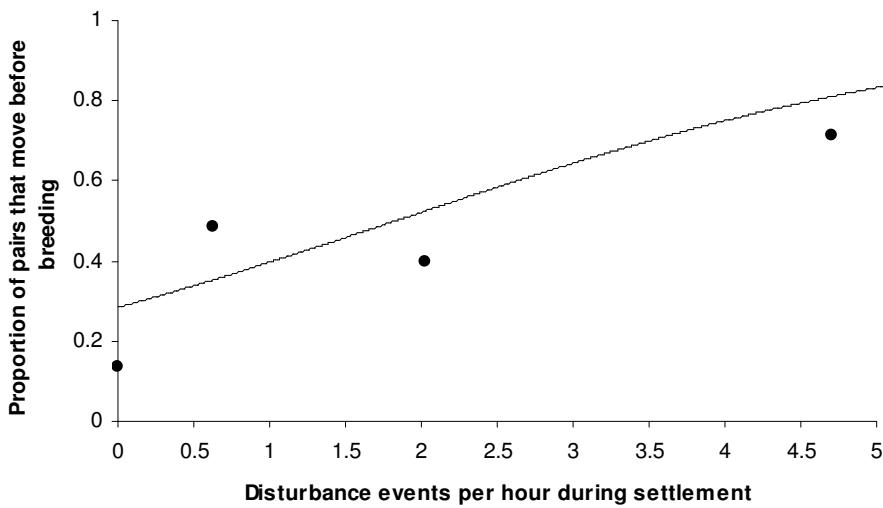


Figure 8.6. Logistic regression model fit (lines) and observed binned data (points) of the probability of a movement between sites during settlement in relation to the disturbance events per hour during settlement.

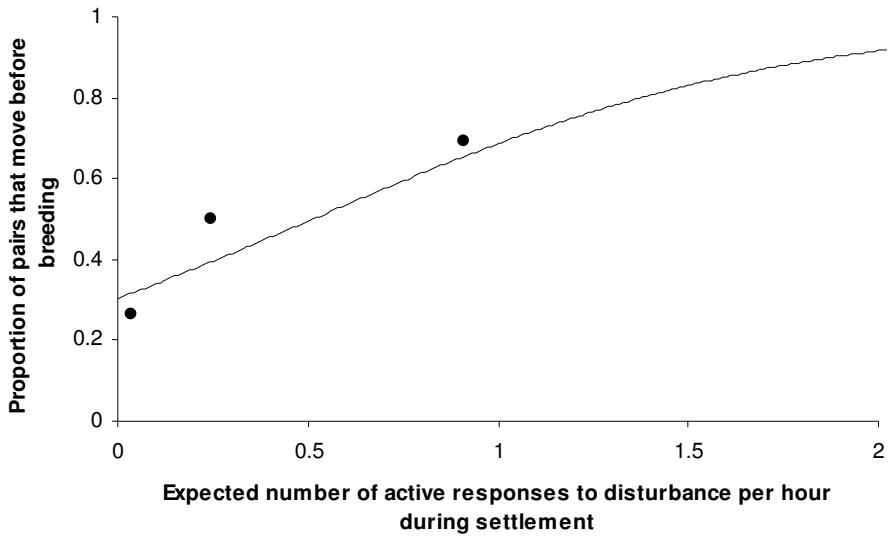


Figure 8.7. Logistic regression model fit (lines) and observed binned data (points) of the probability of a movement between sites during settlement in relation to the expected number of active responses per hour during settlement.

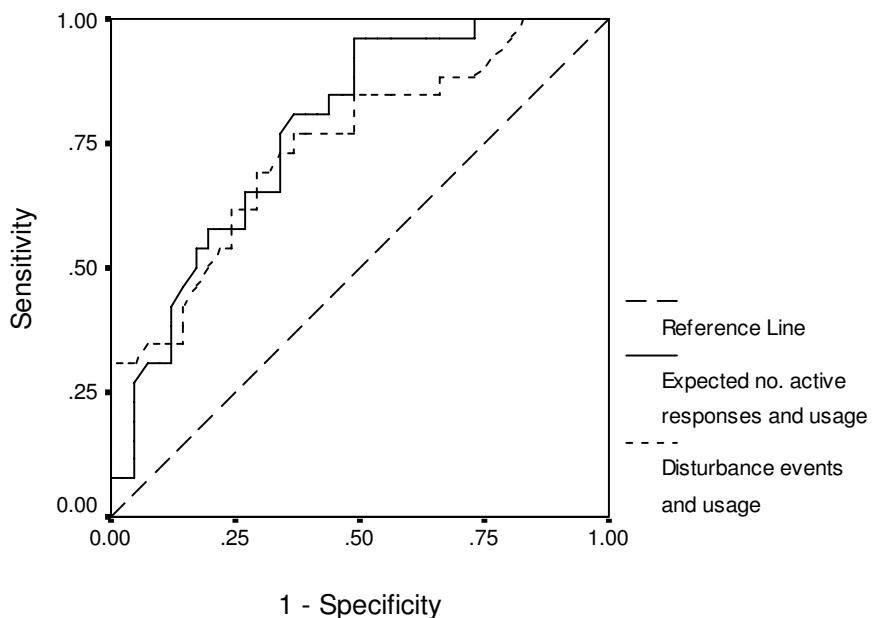


Figure 8.8. Receiver operating characteristics (ROC) curves used to assess the fit of the logistic regression models describing the probability of movement before settlement with expected number of active responses per hour during settlement and historic use by any pair of stone curlews (Table 8.7); and settlement disturbance event rate and historic use by any pair of stone curlews (Table 8.6). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

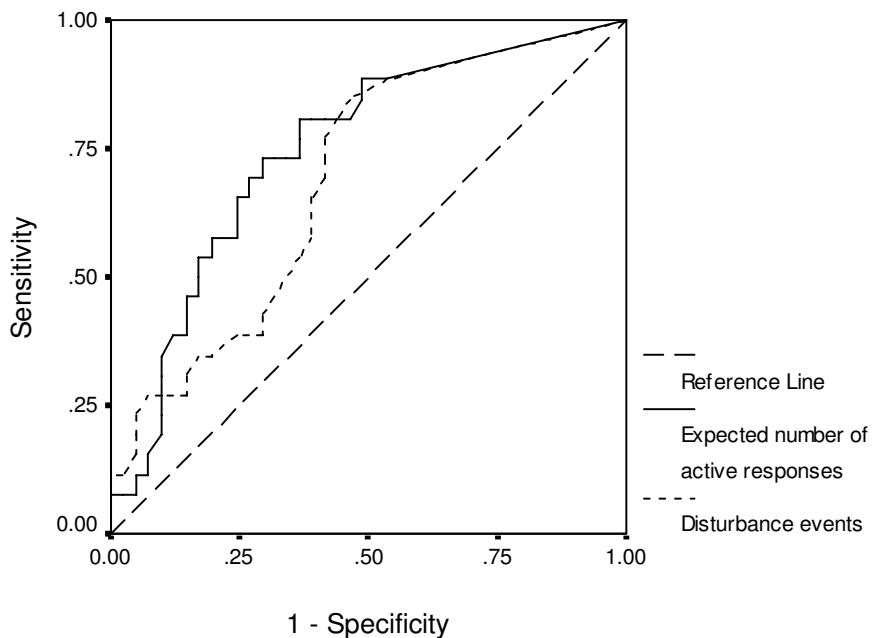


Figure 8.9. Receiver operating characteristics (ROC) curves used to assess the fit of the logistic regression models describing the probability of movement before settlement with expected number of active responses per hour during settlement (Table 8.9); and settlement disturbance event rate (Table 8.8). The diagonal line through 0 indicates the outcome that would be expected if the models were no better than chance at correctly predicting a positive event.

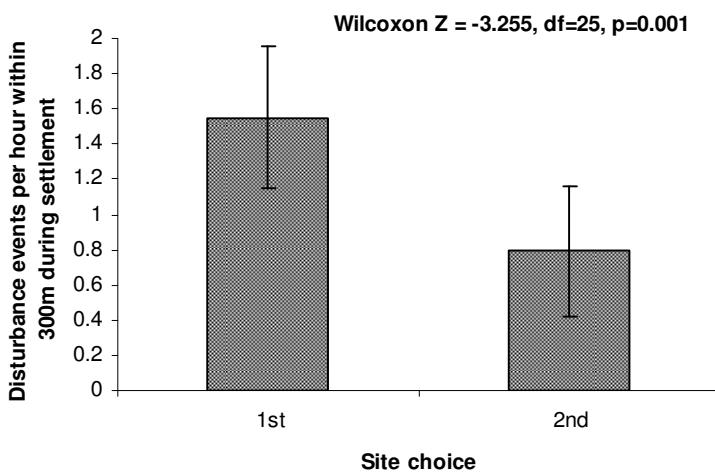


Figure 8.10. There was a significant difference between the first and second choice of plot in terms of disturbance events per hour during settlement

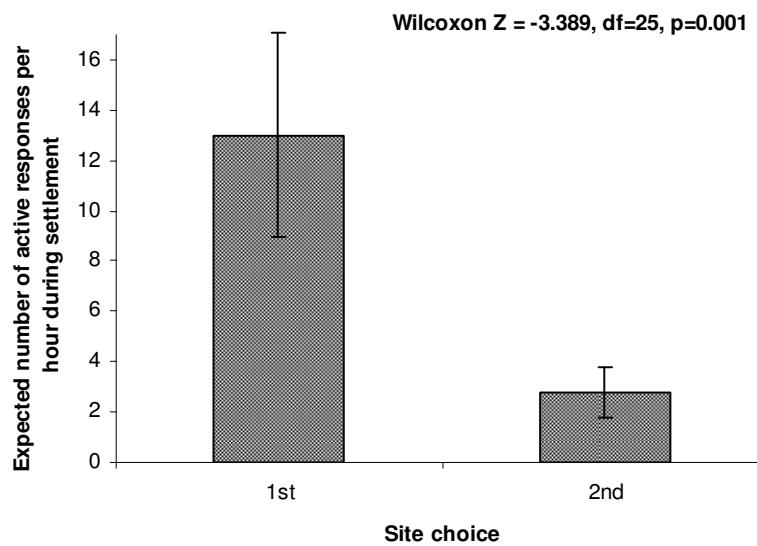


Figure 8.11. There was a significant difference between the first and second choice of plot in terms of expected number of active responses per hour during settlement

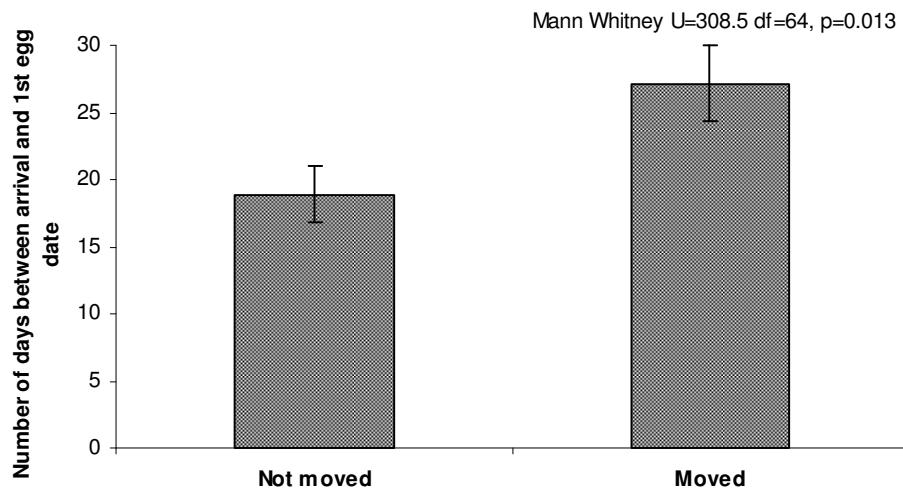


Figure 8.12. There was a significant difference between the time between arrival and first egg date for pairs that moved and those that did not.

Table 8.1. Descriptions of explanatory variables used in analyses. These variables are in addition to those in Chapter 6, Tables 6.1 and 6.2.

Variable	Description
Distance to road of any classification (m)	Shortest straight line distance from the centre of the plot to the nearest road of any classification (m)
Distance to next unoccupied habitat by time of arrival	Shortest straight line distance from the centre of the plot to the next nearest unoccupied habitat (m)
Type of habitat I	Classification of habitat as either a stone curlew plot or a patch of semi-natural chalk grassland
Type of habitat II	Classification of habitat as either a tilled stone curlew plot or a patch of semi-natural chalk grassland/chalk scrape
Arrival date	Days since 1 January colour ringed pair where first located
Age of stone curlew	Age in years of colour ringed bird
Area of suitable breeding habitat	Area of plots within 1km of nest site (ha)
Historic use by any pair	The proportion of years since 1999 (or year plot was created if later) site has been occupied for breeding by stone curlews
Historic use by prospecting pair	The number of years since 1999 (or year plot was created if later) site has been occupied for breeding by the prospecting pair of stone curlews as proportion of number of years this pair has been breeding (assuming first breeding at age two).

Table 8.2. List of candidate explanatory variables used in analyses.

Variable	Variable type
Expected number of active responses per hour during settlement	Continuous
Settlement disturbance event rate	Continuous
Breeding pair visible from focal plot	Factor, 2 levels: Yes=1, No=0
Distance to woodland edge (m)	Continuous
Distance to nearest A road (m)	Continuous
Distance to nearest road of any classification (m)	Continuous
Distance to nearest vehicle accessible track (m)	Continuous
Distance to next occupied plot (m)	Continuous
Distance to next unoccupied plot (m)	Continuous
Distance to nearest village (m)	Continuous
Area of woodland within 1km radius	Continuous
Type of habitat I (plot or semi-natural chalk grassland)	Factor, 2 levels: plot or semi-natural chalk grassland
Distance to core of population (m)	Continuous
Area of suitable feeding habitat within 1km radius (ha)	Continuous
Surrounding habitat	Factor, 2 levels: grassland or arable
Area immediately off plot suitable for feeding	Factor, 2 levels: Yes=1, No=0
Presence of manure heap within 1km radius	Factor, 2 levels: Yes=1, No=0
Aspect	Factor, 4 levels: n, s, e, w
Type of habitat II (tilled plot or semi-natural chalk grassland)	Factor, 2 levels: tilled plot or semi-natural chalk grassland
Area of plot (m^2)	Continuous
Slope of plot	Factor, 2 levels: Yes=1, No=0
Rabbit index	Continuous
Corvid index	Continuous
Year	Factor, 2 levels: 2004 and 2005
Historic use by any pair of stone curlews	Continuous
Historic use by prospecting pair of stone curlews	Continuous
Percentage cover of vegetation at nest scale	Continuous
Percentage bare ground at nest scale	Continuous
Percentage stones <2cm at nest scale	Continuous
Mean vegetation height at nest scale	Continuous
Maximum vegetation height at nest scale	Continuous
Percentage cover of vegetation at intermediate scale	Continuous
Percentage bare ground at intermediate scale	Continuous
Percentage stones <2cm at intermediate scale	Continuous
Mean vegetation height at intermediate scale	Continuous
Maximum vegetation height at intermediate scale	Continuous
Arrival date	Continuous
Age of stone curlews	Continuous

Table 8.3. The number of pairs seen in the settlement period in 2004 and 2005 and the proportion observed to change site.

Year	Number of pairs seen up to 20 th April	Number of pairs observed to move sites	Proportion of total
2004	29	13	0.45
2005	38	13	0.34
Combined	67	26	0.39

Table 8.4. Differences between nest scale habitats at sites where birds moved and did not move. Mean values for pairs that moved and did not move are shown for continuous variables. Significant differences are shown in bold.

Variable	Moved	Not moved	Test
Rabbit index	3.261	2.335	Mann Whitney U=364.0, df=66, p=0.029
Percentage cover of vegetation	0.101	0.075	Mann Whitney U=462.5, df=66, p=0.231
Percentage bare ground	0.902	0.934	Mann Whitney U=462.5, df=66, p=0.233
Percentage stones <2cm	0.123	0.112	Mann Whitney U=528.5, df=66, p=0.945
Mean vegetation height mm	0.161	0.053	Mann Whitney U=423.5, df=66, p=0.0701
Maximum vegetation height mm	0.365	0.185	Mann Whitney U=432.5, df=66, p=0.0972
Area of habitat block ha	160097.856	144619.832	Mann Whitney U=406.0, df=66, p=0.131
Type of habitat 1 (plot or SNCG)			Fishers exact test p=0.291
Type of habitat 2 (tilled or chalk)			$\chi^2=1.81$, df=1, p=0.171
Aspect			Fishers exact test p= 0.412
Slope			$\chi^2=0.05$, df=1, p=0.811

Table 8.5. Differences between intermediate and landscape scale variables at sites where birds moved and did not move. Means are shown for continuous variables. Significant variables are shown in bold.

Variable	Moved	Not moved	Test
Proportion of years site has been used by any pair	0.564	0.764	Mann Whitney U=348.0, df=66, p=0.0163
Percentage cover of vegetation at intermediate scale	89.032	93.904	Mann Whitney U=45.5, df=66, p=0.434
Percentage bare ground at intermediate scale	10.004	6.094	Mann Whitney U=498.0, df=66, p=0.464
Percentage stones <2cm at intermediate scale	0.964	0.00	Mann Whitney U=492.0, df=66, p=0.0744
Mean vegetation at intermediate scale mm	4.614	5.972	Mann Whitney U=520.0, df=66, p=0.823
Maximum vegetation height at intermediate scale mm	6.652	7.582	Mann Whitney U=524.0, df=66, p=0.505
Arrival date	38074.851	38077.904	Mann Whitney U=519.5, df=66, p=0.866
Area of suitable breeding habitat in 1km radius ha	13.001	8.121	Mann Whitney U=388.0, df=66, p=0.0552
Area of suitable feeding habitat in 1km radius ha	239.123	208.483	Mann Whitney U=413.5, df=66, p=0.121
Area of woodland in 1km radius ha	13.263	18.295	Mann Whitney U=491.5, df=66, p=0.584
Distance to woodland edge m	327.305	419.144	Mann Whitney U=407.5, df=66, p=0.102
Distance to A road m	1707.693	1490.004	Mann Whitney U=462.5, df=66, p=0.361
Distance to any classification of road m	1290.386	1158.532	Mann Whitney U=493, df=66, p=0.603
Distance to track m	337.386	508.652	Mann Whitney U=429.0, df=66, p=0.183
Distance to nearest village m	2011.534	2043.904	Mann Whitney U=499.5, df=66, p=0.663
Distance to next occupied plot by time of arrival m	770.561	907.193	Mann Whitney U=400.5, df=66, p=0.088
Distance to next unoccupied plot at time of arrival m,	1405.251	1358.233	Mann Whitney U=444.5, df=66, p=0.253
Distance to core of population m	97.496	962.564	Mann Whitney U=446.0, df=66, p=0.261
Breeding pair visible from focal plot			Fisher's Exact test p=0.099
Presence of manure heaps within 1km radius			$\chi^2=0.16$, df=1, p=0.681
Surrounding habitat			$\chi^2=3.41$, df=1, p=0.0641
Area around plot suitable for feeding			$\chi^2=3.01$, df=1, p=0.0781

Table 8.6. MAM of the probability of a movement between breeding sites by stone curlews during settlement (using settlement disturbance event rate). Shown are the parameter estimates and the reduction in deviance from having the variable in the model and associated p values. The residual deviance of the model is 76.3687 with 64 degrees of freedom

Variable	Parameter estimate	SE	Reduction in residual deviance	df	P
Intercept	0.6862	0.7342			
Settlement disturbance event rate	0.4738	0.2387	5.30	1	0.0214
Recent use by any pair	-2.3447	0.9791	6.17	1	0.0131

Table 8.7. MAM of the probability of a movement between breeding sites by stone curlews during settlement (using the expected number of active response per hour during settlement). Shown are the parameter estimates and the reduction in deviance from having the variable in the model and associated p values. The residual deviance of the model is 76.85 with 64 degrees of freedom

Variable	Parameter estimate	SE	Reduction in residual deviance	df	P
Intercept	0.8530	0.7148			
Expected number of active responses per hour during settlement	1.4123	0.7768	4.82	1	0.0281
Recent use by any pair	-2.4525	0.9602	7.10	1	0.00771

Table 8.8. The probability of a movement between breeding sites by stone curlews during settlement in relations to the settlement disturbance event rate. Shown are the parameter estimates and the reduction in deviance from having the variable in the model and associated p values. The residual deviance of the model is 82.54 with 65 degrees of freedom.

Variable	Parameter estimate	SE	Reduction in residual deviance	df	P
Intercept	-0.9242	0.3238			
Settlement disturbance event rate	0.5057	0.2286	6.95	1	0.00831

Table 8.9. The probability of a movement between breeding sites by stone curlews during settlement in relation to the expected number of active responses per hour during settlement. Shown are the parameter estimates and the reduction in deviance from having the variable in the model and associated p values. The residual deviance of the model is 83.95 with 65 degrees of freedom.

Variable	Parameter estimate	SE	Reduction in residual deviance	df	P
Intercept	-0.8240	0.3092			
Expected number of active responses per hour during settlement	1.6072	0.8154	5.54	1	0.0181

Table 8.10. AUC values from ROC curves assessment of model performance in successfully classifying pairs which did or did not move during the settlement period..

Model	Table	AUC	SE	P
Settlement disturbance event rate	6	0.68	0.06	0.0091
Expected number of active responses per hour during settlement	7	0.74	0.06	0.0011
Settlement disturbance event rate and recent use by any pair	8	0.74	0.06	0.001
Expected number of active responses per hour during settlement and recent use by any pair	9	0.77	0.05	<0.0001

Table 8.11. Correlations between disturbance variables and other explanatory variables.
Significant correlations are shown in bold.

	Distance to next occupied habitat (m)	Area of suitable feeding habitat within 1km (ha)	Distance to A road (m)	Distance to any road (m)	Distance to track (m)	Distance to village (m)
Disturbance event rate	r -0.29	0.29	0.54	0.54	-0.30	0.20
	p 0.016	0.017	<0.0001	<0.0001	0.011	0.09
	n 67	67	67	67	67	67
Expected number of active responses per hour during settlement	r -0.5	0.18	0.03	0.09	-0.04	-0.19
	p 0.66	0.13	0.80	0.43	0.71	0.12
	n 67	67	67	67	67	67

Table 8.12. Differences between first choice of site and second choice. Means for continuous variables are shown. Significant variables are highlighted in bold.

Variables	Mean 1 st choice	Mean 2 nd choice	Test
Expected number of active responses per hour during settlement	0.40	0.09	Wilcoxon z=-3.389, df=25, p=0.0011
Settlement disturbance event rate	1.55	0.79	Wilcoxon z=-3.255, df=25, p=0.0014
Distance to next occupied habitat m	770.57	900.92	Wilcoxon z=-2.654, df=25, p=0.0082
Area of additional breeding habitat within 1km radius ha	13.00	2.77	Wilcoxon z=-2.417, df=25, p=0.021
Maximum vegetation height at intermediate scale mm	6.65	4.92	Wilcoxon z=-1.959, df=25, p=0.0498
Percentage cover of vegetation at nest site scale	0.19	0.069	Wilcoxon z=-0.767, df=25, p=0.444
Percentage bare ground at nest site scale	0.90	0.93	Wilcoxon z=-0.767, df=25, p=0.443
Percentage stones <2cm at nest site scale	0.12	0.10	Wilcoxon z=-0.684, df=25, p=0.496
Mean vegetation height at nest site scale mm	0.16	0.10	Wilcoxon z=-0.940, df=25, p=0.357
Maximum vegetation height at nest site scale mm	0.36	0.19	Wilcoxon z=-1.414, df=25, p=0.168
Area of habitat block ha	16.8	22.0	Wilcoxon z=-0.114, df=25, p=0.916
Rabbit index	3.26	3.32	Wilcoxon z=-0.336, df=25, p=0.744
Percentage cover of vegetation at intermediate scale	92.88	93.84	Wilcoxon z=-0.175, df=25, p=0.862
Percentage bare ground at intermediate scale	7.11	5.57	Wilcoxon z=-0.351, df=25, p=0.735
Percentage stones <2cm at intermediate scale	0.00	0.57	Wilcoxon z=-1.342, df=25, p=0.186
Mean vegetation height at intermediate scale mm	4.76	4.30	Wilcoxon z=-0.614, df=25, p=0.548
Area of suitable feeding habitat within 1km radius ha	239.12	228.80	Wilcoxon z=-1.517, df=25, p=0.138
Area of woodland within 1km radius ha	13.26	19.52	Wilcoxon z=-1.912, df=25, p=0.066
Distance to woodland edge m	327.30	289.53	Wilcoxon z=-1.029, df=25, p=0.305
Distance to A road m	1707.69	1496.15	Wilcoxon z=-1.279, df=25, p=0.203
Distance to any classification of road m	1290.38	1128.84	Wilcoxon z=-1.509, df=25, p=0.135
Distance to track m	337.38	375.84	Wilcoxon z=-0.025, df=25, p=0.987
Distance to nearest village m	2011.53	1700.00	Wilcoxon z=-1.817, df=25, p=0.079
Distance to next unoccupied plot at time of arrival m	1397.19	1372.76	Wilcoxon z=-0.927, df=25, p=0.356
Distance to core of population m	979.49	1017.13	Wilcoxon z=-0.648, df=25, p=0.524
Recent use by any pair	0.56	0.46	Wilcoxon z=-0.872, df=25, p=0.382
Recent use by prospecting pair	0.18	0.09	Wilcoxon z=-1.261, df=10, p=0.211
Corvid index	5.25	4.23	Wilcoxon z=-1.372, df=25, p=0.177

Table 8.13. Differences in breeding parameters between sites where stone curlews moved and did not move.

Variable	Moved	Not moved	Test
Mayfield probability of survival through incubation period for first nesting attempt	0.5542	0.6234	Mann Whitney U=443.5, df=64, p=0.491
Chicks fledged per nesting attempt	0.40	0.29	Mann Whitney U=422.0, df=64, p=0.255
Chicks fledged per season	0.46	0.42	Mann Whitney U=439.0, df=64, p=0.384

9 General discussion and management implications

9.1 Introduction

After the introduction of the Countryside and Rights of Way Act 2000, Liley (2001) stressed that there was a need for targeted, good quality research into the effects of disturbance on bird populations. Despite effects of human disturbance on wildlife being one of the most prolific areas of conservation research, it was clear that the available information was not adequate for decisions makers. In particular, English Nature (now Natural England) has powers to close to public access areas of open land that would otherwise be open under the Act. It is not obvious how the published information on the disturbance of birds can be used to decide which areas should be closed to protect birds. This is because disturbance studies vary vastly in their subjects, objectives, methods and results cannot be easily extrapolated to other species (Sidaway, 1990). One of their major weaknesses is that many simply report the sensitivity of birds to human disturbance, in terms of their observed flight response, but do not consider further how that can affect resource use (Gill *et al.*, 2001). Furthermore, very few studies make specific evidence-based recommendations about the management of access based upon anything other than flight responses.

The CRoW Act, and changes in military training on Salisbury Plain, drew attention to the potential susceptibility of stone curlews to human disturbance. The available disturbance literature was not sufficient to manage potential disturbance to one of England's rarest breeding birds. Therefore, the overall aim of this thesis was to establish the extent to which human disturbance affects stone curlews and make suggestions for management. I achieved the first part of this aim in three ways. Firstly, I examined changes in behaviour in response to human disturbance using the traditional per event method and a new logistic modelling approach. I secondly, looked at the settlement and use of breeding plots by stone curlews with respect to measured disturbance levels. I thirdly, studied the effect of disturbance on breeding parameters. The second part of the aim was achieved through a collaboration to produce a software tool for land managers. Although I have discussed the significance of results in individual chapters, I begin this discussion by summarising the main findings of the study. I then discuss the significance of the study in the wider context of stone curlew conservation and suggest how the tool can aid the implementation of the results from this study. Finally, I comment on future stone curlew research.

9.2 Summary of main results

In Chapter 2 I showed that two experts on stone curlew nesting plots overestimated the level of disturbance, and in particular did not recognise undisturbed sites. This is important because such perceptions affect the creation of new stone curlew nesting sites. Nesting plots have not been created in some areas because they were thought to be too frequently disturbed. My findings indicate that there might be areas with little disturbance in which new plots could be occupied by nesting stone curlews. As a short-cut to identifying such areas, I attempted to produce models which could predict human disturbance, based on possible correlates of disturbance such as proximity to villages and access points. Possible disturbance correlates are widely used in disturbance studies (e.g. Donazar *et al.*, 1993, Moran-Lopez *et al.*, 2006) and if successful, they are extremely powerful in the management of access where real estimates of disturbance are difficult to obtain. Furthermore, they were one of the targets set by Liley (2001) as being priorities for research. Unfortunately, there were few correlates between variables such as distance to village or distance to access points, and recreational disturbance in my study. This was mainly a result of my sites being plots in arable fields or on SPTA and there being no formal access points, such as car parks. However, it may also be a result of disturbance levels being extremely low in the study area and any relationships being very weak, or an inadequacy in the methods used to measure disturbance (see 9.6). Predictive models of military disturbance, however, were possible. Military disturbance was correlated quite strongly with tracks, access points and proximity to a major training site. As a result, the military model may be used to manage military training, target areas for future stone curlew sites and may be helpful in the placement of new access points and tracks with respect to stone curlew plots.

In Chapter 3 I showed that stone curlew behaviour was very sensitive to human disturbance. Response distances were shown to be significantly larger than in other waders (e.g. Flemming *et al.*, 1988, Yalden and Yalden, 1990), and more like those found in raptors (e.g. Gonzalez *et al.*, 2006, Arroyo and Razin, 2006). Most PDA events caused an alert response by stone curlews but over a third also caused an active response whereby the stone curlew moved away from the breeding plot. In common with other studies, differences between PDA types were observed (e.g. Gonzalez *et al.*, 2006; Richardson and Miller, 1997), with people walking on foot and with a dog producing a greater probability of active responses compared with disturbance by a vehicle. However, there were many other aspects to do with the PDA event, such as the stage of breeding, closest approach and route, which were also significant in the models to predict a response. Average response distances and models of response probability based on response distances, are

often suggested for the management of disturbance at sites (e.g. e.g. Arroyo and Razin, 2006, Gonzalez *et al.*, 2006, Fernandez-Juricic *et al.*, 2001). However, we show that there is more associated with the PDA event that determines whether a stone curlew will respond or not. As a result, management of stone curlew sites based on these methods could over- or under estimate the effect of the disturbance. To improve these analyses, in Chapter 4 we developed a new method that modelled the probability of response for each linear segment of the route travelled by the PDA. This method takes into account attributes of the PDA, such as speed and distance from the bird, that vary at different stages of the route. Many of the factors associated with the probability of a response to a PDA are likely to be similar to evolved anti-predator responses.

In Chapter 5, the models from Chapter 4 were used to derive a more meaningful measure of disturbance than the disturbance event rate described in Chapter 2. Models describing the probability of an active response were applied to mapped data on PDA events to convert all observed PDA events into an expected probability of an active response. These probabilities were then used to convert PDA event rates to expected numbers of active responses per unit time. This gives a measure of disturbance that effectively takes into account variation in PDA types and routes. This is preferable to a simple rate of PDA events approaching the site within a specified distance, because the distance of closest approach may vary enormously among sites and events if the qualifying distance for inclusion is set large enough to include all events that might cause a response. This variable was then used in subsequent analyses of breeding success and distribution.

However, if the thesis has restricted itself to modelling behavioural responses, the thesis would deserve the same criticism of many disturbance studies; that it does not consider possible effects on population processes. Therefore, it was important to consider how human disturbance affects other aspects of stone curlews in the breeding season, such as distribution, settlement and breeding success.

Selection of sites for breeding is usually a trade-off between food availability and the risk of predation of the parents or their offspring (e.g Valkama, Robertons and Currie, 1998). I showed in Chapter 6 that breeding sites with low disturbance frequency and where there was a lower expected rate of active responses were more likely to be used for nesting by stone curlews. This is presumably because of a larger perceived predation risk to itself, eggs or chicks as a result of human activities. In addition, other factors influenced plot choice. Stone curlews selected plots

away from A roads and woodland edges and avoided the smallest plots and those from which other breeding pairs were visible. I also showed how the behavioural models from Chapters 4 and 5 could be combined with the plot occupancy models in Chapter 6 to produce a management tool for access decisions under CRoW (discussed further in section 9.4).

Decisions made during settlement about where to breed were investigated in Chapter 8. Using colour ringed adults, it was shown that 40% of pairs do not lay their first clutch of the season on the nesting plot on which they first arrived in early spring. Pairs were significantly more likely to move plots during settlement where both PDA event rate and the expected number of active responses was high. Furthermore, the second site chosen was less disturbed in both respects. This is possibly evidence of stone curlews showing adaptive plasticity in nest site choice through information gathering to assess suitability before breeding.

Stone curlews may avoid the most disturbed plots because there is a perceived risk of predation that they associate with human activity. However, unless this risk is real and there is an effect of human disturbance on breeding success, such avoidance is psychological and is not adaptive under current conditions. In this case, avoidance may adversely impact breeding success because birds may be forced to move to less suitable sites in terms of habitat quality or suffer competition with other pairs for breeding plots. Alternatively, there may be enough good quality alternative plots for the avoidance of disturbed plots to have no impact on breeding success. However, even if the latter situation prevails, with a growing population or loss of habitat, breeding success could be affected in the future. Therefore, in Chapter 7 I examined the effect of disturbance on breeding success in the Wessex population. No clear adverse effects of human disturbance were found. Chicks appeared to grow slower on more disturbed plots, possibly as a result of less provisioning or reduced brooding by the adults (Yalden and Yalden, 1990), but this had no influence on chick survival. There was also no apparent effect of disturbance on nest success, chick fledging rate, chick survival, the probability of re-nesting after egg stage failures, or timing of breeding. This either suggests that there are few adverse impacts of disturbance on breeding success, or it could be a product of stone curlews already selecting against the most disturbed plots. Variation in disturbance levels among plots used by stone curlews is low, so impacts on breeding success may not be easy to detect for that reason.

9.3 Significance of results in wider context of stone curlew conservation

The stone curlews breeding in England are representatives of the population at the very northern edge of their range. Indeed, this population is further from the equator than any other population of species in the family Burhinidae. Population declines over much of Europe mean that stone curlews are of conservation concern throughout their range. Due to their dependence on very specific soil types and habitats, stone curlew were never found everywhere in England, but they were certainly more numerous than today and also more widespread (Holloway 1991). Following the massive population crash, the population would not have recovered to today's levels without conservation action, which was led by RSPB and English Nature. Intensive conservation input delivered through the Recovery Project, involving nest and chick protection and the creation of nesting habitat, allowed the population to recover to over 300 breeding pairs in 2005 – the 2010 BAP target five years in advance (Wynde, 2006). The Stone Curlew Recovery Project is a very clear example of how targeted conservation effort can turn around the decline of a species. However, there is a need for continued conservation effort to increase the population further and expand the current range and well targeted research of stone curlew breeding biology and habitat preference can help assist in the recovery.

In Wessex, suitable nesting habitat is delivered as artificially created 1-2 ha stone curlew plots and a priority is how to maximise the use of these. Most stone curlew plots are administered through agri-environment schemes. Farms in the Entry Level Scheme can apply for Higher Level payments to create a fallow plot for ground nesting birds (option HF13 or enhanced set-aside option HF17), specifically targeted at stone curlews. Land owners are advised where to place plots in order to maximise potential use by stone curlews but the advice is not derived from any formal evidence base. Given that expert opinions about disturbance are not always accurate, better information on the effects of disturbance can be useful here. Results of this and other studies should be used to improve the effectiveness of agri-environment schemes for stone curlews. For example, the plot occupancy model from Chapter 6 showed that plots were less likely to be used if near A roads as found in previous studies by Day (2003) and Green *et al.* (2000). Other factors such as distance to woodlands and visibility of other breeding pairs should also be taken into account, as well as consideration of human disturbance. Ways to assess the effects of human disturbance when considering plot locations are discussed in section 9.4.

However, whilst extremely successful in increasing the numbers of breeding stone curlews, perhaps the present type of stone curlew plot should not be considered the final solution to the

problem of habitat loss. At present stone curlew plots are small and well spaced in the landscape. They are created at a farm level and a farm may have just one, so spacings are determined by the uptake of agri-environment schemes by farmers and the size of their farm holdings. As a result, we are effectively controlling densities of nesting pairs at much lower levels than those on semi-natural chalk grassland. This could have consequences for the population if stone curlews benefit from breeding in closer proximity to other pairs. Stone curlew plots probably already make stone curlews more vulnerable to predation. It is possible that they are more vulnerable to disturbance on plots too. My study was based around plots and there were not enough arable crop or semi-natural grassland nesting pairs in my study area to assess any differences in response to behaviour in different habitats.

It may be more desirable to create larger areas of nesting habitat so that stone curlew densities in artificially created habitat can mimic that on semi-natural habitat to a greater extent. This may be achieved through reversion of arable land back to semi-natural grassland. Again, arable reversion payments are available to landowners through Higher Level agri-environment schemes. This is, however, probably more of a long term solution as it takes several years for arable reversion to mimic the type of grassland favoured by stone curlews (E.C. Taylor, pers, obs). However, plots within grassland can be considered similar to nesting actually on grassland so arable reversion increases the potential for this. Furthermore, arable reversion can provide additional feeding habitat. The RSPB has recently demonstrated its commitment to stone curlew conservation in Wessex through increasing habitat management at a larger scale. A management agreement on land near Stonehenge – RSPB Normanton Down – will see the reversion of arable land back to grassland for the benefit of stone curlews and other chalk grassland species. Furthermore, the purchase of a new reserve – RSPB Manor Farm – on the edge of DSTL Porton Down will provide additional nesting habitat and arable reversion for stone curlews. The efforts of individual landowners must also be highlighted and one farmer can be singled out for his outstanding efforts and vision in creating suitable habitats for stone curlew, and other species, on his land. Henry Edmunds' land at Cholderton Estate is critical to stone curlew conservation as it provides the geographical link between the last remaining large tracts of semi-natural chalk grassland on SPTA and DSTL Porton Down. The work achieved on this land to maximise the benefit of this link includes several hundred hectares of arable reversion. Some of the reversion now mimics the semi-natural chalk grassland on Porton Down to such an extent that I predict it will not be long before stone curlews nest on the grassland rather than the plot nearby.

Availability of funds for stone curlew habitat creation needs consideration. The implementation of DEFRA Entry and Higher Level schemes gives a long term future to funding. Additionally, the prescriptions are flexible enough to provide the specific habitat needed for stone curlews. The wider biodiversity benefit of stone curlew nesting plots, in terms of invertebrates, rare arable plants and other birds, is currently the subject of a RSPB research project. Conservation which targets a particular species but also benefits other species as a by-product is desirable and would possibly secure funding of additional suitable habitat. However, agri-environment schemes targeted at stone curlews should do just that and their value should not be determined by additional benefits, even though any additional benefits are clearly a bonus. From a personal point of view I see no problem with a single species targeted agri-environment scheme for a rare, range restricted species such as the stone curlew.

Changes in countryside access and military training present new challenges for stone curlew conservation in the UK. However, it is suggested that the methods presented in this thesis can be used to manage the changes to minimise impacts on stone curlews, whilst providing access to the countryside.

9.4 Management of access on stone curlew breeding habitat

The study clearly shows that some plots are avoided for breeding if PDA events of types which cause an active response occur frequently. Currently, disturbance on the plots used for breeding does not appear to be affecting the productivity of stone curlews directly. However, as the population continues to recover and there is no alternative habitat to disturbed sites, the impact on the population is not known. It is also possible that breeding success on some sites that are avoided because of disturbance would be higher than these pairs achieve on the plots they actually use. The results presented in this thesis, therefore, should be used to manage access near stone curlew breeding plots and further improve the siting of new plots.

Many disturbance studies make recommendations for management of access based on mean flushing distance. These recommendations usually involve buffer zones or set-back distances where disturbance is excluded within a certain distance (Rodgers & Schwikert 2002, Richardson & Miller 1997, Rodgers & Smith 1995). We suggest that, for stone curlew sites, management planning can go beyond buffer zones and set-back distances.

The models described in this thesis can provide data of practical value to users interested in the impact of specified patterns of disturbance. Firstly, the vehicle and non vehicle active response models from Chapter 4 can be used to quantify the per unit distance travelled probability of a stone curlew responding actively to any PDA event with specified characteristics. Then, using the method in Chapter 5, the probability of response per *event* is calculated. Secondly, by specifying the likely frequency of PDA events of each type, the models can be used to obtain expected rates at which responses are shown (*expected number of active responses per hour*). Finally, using the plot occupancy model which relates the expected number of active responses to the probability of plot use, the likelihood of sites being occupied by stone curlews can be obtained.

As this is quite complicated to work out for real sites, to aid the evaluation of the impact of specified disturbance at real sites, the statistical models have been incorporated into a software package known as the Stone Curlew Access Response Evaluator (SCARE). The project was a collaboration between myself, Rhys Green (RSPB) and James Perrins (exeGesIS Spatial Data Management Ltd) and was funded by RSPB and EN. SCARE is a user-friendly interface with the behaviour and plot occupancy models embedded behind. The user can take a built-in map, digital terrain model and information on screening vegetation for a real site and explore the consequences of various patterns of access to that site (e.g. different disturbance types and frequencies, path or track routes) and various mitigation measures (e.g. closure of areas, additional screening with boards or hedges, redirection of paths, relocation of stone curlew nesting plots). PDA types covered by SCARE are walkers, walkers with dogs, motor vehicles (including military vehicles), joggers, cyclists and horse-riders. The user can specify stone curlew locations (e.g. nest sites) using real location data or proposals for the creation of artificial nesting plots. The user can also specify and alter routes likely to be used by PDAs, and PDA types and frequencies.

Outputs from the software include a map of the site showing the “viewshed” (the area around the breeding site within which PDAs are visible to the bird). The user can specify routes taken by PDAs by dragging the cursor across the map, and classifies the type or mixture of PDA types and the frequency of events. The programme then uses the imbedded behaviour model to calculate the expected rate at which a stone curlew would make active responses to the PDAs described. Finally, SCARE uses the empirical relationship between plot occupancy and the modelled rate of disturbance to estimate the expected reduction in the probability of the plot being used by nesting stone curlews, compared with what would be expected with no disturbance (Figure 9.1).

The impact of changing the disturbance scenario can then also be explored. For example, the user can change the type and frequency of PDAs, the location of an access route, the location or size of an open access or closed area, or the location of screening vegetation (Figure 9.1), and obtain revised estimates of the impact on stone curlews. The effect of changing the location of the stone curlew plot can also be evaluated, which is of applied value because of the ease in which landowners can create stone curlew habitat.

We feel that SCARE reconciles the need for public access to open landscapes with the need for continued conservation of stone curlews at existing and future potential breeding sites. It offers a way to assess the effects of hypothetical scenarios for future changes in disturbance type, routes and frequency, including the manipulation of disturbance levels. We hope that this tool will be valuable in informing decisions concerning areas to be opened up for access or closed for part of the year when stone curlews are breeding. Also SCARE can improve the effectiveness of agri-environment schemes targeted at stone curlews through assessing potential sites with respect to disturbance and helping select the most appropriate location for new habitat. Furthermore, whilst SCARE is currently a single species tool, we feel it provides a framework by which other species could be assessed if data is available for the modelling procedure.

In the process of developing SCARE we arranged a meeting with likely ‘customers’ of the tool to gather input on the usefulness of the tool. SCARE still requires that the disturbance regime (frequency and types of PDAs) is known at a site and concerns were raised as how to measure the disturbance at a site. However, it is suggested that with any management solution the disturbance regime should be known and time should be spent collecting this. Future predictive models could help with estimations. I will also be working on this issue further by summarising the methods used in my study to measure disturbance and producing information on the minimum time to spend at a site to gather an accurate average estimate.

SCARE has now (2006) been delivered to the customers who will use it in RSPB and EN and can be used to assess the placement of new nesting plots. Furthermore, it will be used to assess the risk from disturbance on Breckland heathland sites, and will be used in a study to predict the impacts of changes in military disturbance on SPTA.

9.5 Changes in countryside access

An important question is: will recreational disturbance actually increase on stone curlew sites as a result of CRoW? Recent research suggests that changes to visitor number to the countryside may be quite small (MVA, 1999). Additionally, changes in access are likely to be related to the amount of publicity given to sites, signposting of paths and the attractiveness of visiting, in terms of visitor car parks, information points, toilets and cafes. Of stone curlew nesting habitats, the CRoW Act only applies to semi-natural grassland sites and heathland. In Wessex the only semi natural grassland sites with breeding stone curlews currently are on Salisbury Plain Training Area and DSTL Porton Down. Porton Down will not become open to the public due to its use as a high security research facility. Access on SPTA West and Centre will not change due to their role as live firing ranges. SPTA East may see an increase in visitor numbers because new roads are to be built, but lack of parking facilities and the danger of using a military training area for recreation may put visitors off. However, CRoW is not the only issue or cause of change in disturbance. There are plans for increased housing in the south of England and a priority for this is around Salisbury Plain (www.opsi.gov.uk). In this case, the ability to predict new levels of disturbance using predictive models and site attributes (Chapter 2) becomes even more necessary. Such predictive models can be used with SCARE to establish likely levels of disturbance and the subsequent effect on plot occupancy, to manage disturbance and habitat creation. Therefore, as far as possible, projected future changes in disturbance should be taken into account when creating new nesting habitat for stone curlews.

Ironically, some of the closest approaches to stone curlews observed in this study were by bird watchers. This is by no means the fault of the bird watchers, as the sensitivity of stone curlews to human presence may not be realised. However, perhaps this is an issue that needs to be addressed. This problem is exacerbated by there being no reserves in Wessex at which breeding stone curlews can be viewed from hides. In Breckland, visitors can view stone curlews from the comfort of hides at Weeting Heath Norfolk Wildlife Trust reserve. This largely (although not completely) prevents other stone curlew breeding sites getting disturbed in Breckland. It is possible that a similar viewing facility may eventually be possible at RSPB Manor Farm once regular breeding pairs are established, which may reduce this problem.

Most of the changes in disturbance through CRoW may be on chalk grassland sites currently beyond the current range of stone curlews. These include the Marlborough Downs, Pewsey Downs, Chalke Valley grassland, and sites towards Stockbridge. Many of these are already

heavily used for recreation but this may increase with CRoW. Range expansion is a priority in stone curlew conservation so access and habitat on these sites needs to be considered too. Even further afield, there are areas which could support breeding stone curlews in the Chilterns and the South Downs. Both of these areas are heavily disturbed in parts and careful consideration should be taken as to where to create suitable stone curlew nesting habitat if these sites are to be colonised.

It may be significant that within the current range in Wessex there are two sites of semi-natural chalk grassland without breeding stone curlews despite having suitable nesting habitat and breeding stone curlews nearby. These are the National Nature Reserves of Martin Down on the Wilts/Dorset border, and Parsonage Down just off Salisbury Plain West. These two reserves were not in the study area for the main part of this study, but pilot disturbance surveys were carried by me in 2003. Until 2003 Martin Down had a long history of breeding stone curlews. However, the female of the regular pair did not return in 2003 (she would have been 18 years old in 2003) and there has been no breeding in the four years since. Access levels are approximately six PDA events per hour at Martin Down (2003 surveys), well above the rates observed at any stone curlew sites in this study, and consisted almost entirely of dogwalkers. Whilst the regular stone curlew pair may have become habituated to the high disturbance levels, attraction of a new breeding pair may be difficult because of the current disturbance regime. Parsonage Down is also open to public access, and although does not have as high rates as Martin Down (approximately 0.5 PDA events per hour), also does not have breeding stone curlews. Increasing the proportion of grassland nesting stone curlews is a priority in the UK BAP for stone curlews (www.ukbap.org.uk/ukplans) and colonisation of these seemingly suitable sites (in other respects) would greatly assist in the achievement of this goal. It may be that SCARE should be used at these sites to optimise the placement of plots or paths so that stone curlews can return to breed.

How is military training likely to change on SPTA? Given the increasing reliance on air-based warfare, helicopter training activity may increase on SPTA. Although not measured explicitly in this study, other than when making ‘accidental’ landings directly on plots, helicopters were not observed to cause active responses by stone curlews. Furthermore, aeroplane disturbance does not appear to be of concern either, as demonstrated by the habituation of stone curlews nesting near the RAF Lakenheath runway in Breckland. Furthermore, vehicular disturbance is likely to increase. The results from this study show that vehicle disturbance is less likely to cause active responses by stone curlews and the impact of vehicle PDA events on nest site occupancy is quite

low. Even if vehicular disturbance does not significantly affect stone curlew nest choice, the necessity for metalled tracks for tanks on SPTA East opens up areas for other disturbance, including walking. SCARE is currently being used to assess the likely effects of new tracks on SPTA East with respect to military disturbance, but consideration of increases to recreational disturbance will also be made.

Although predictive models of military disturbance were possible in my study, it was my view that military disturbance was actually more sporadic and harder to predict. In particular, when large battle groups or stationary camps are involved there is a potential for greater disturbance and damaging consequences. These were not adequately measured in this study but should be considered in the future.

9.6 Limitations of results

Throughout this study the method of measuring disturbance has been presumed to be adequate. In all three fieldwork years, I experimented with ways to measure human disturbance. These included sand strips, nest cameras, nest temperature loggers and beam counters across paths. However, as can be seen from their absence in this study, none of these were considered adequate for producing reliable disturbance estimates at sites. As a result, I used the 1-hour watches described, which have been used with success in many other studies (Ruhlen *et al.*, 2003, Liley, 1999, Mallord, 2005, Taylor, 2002). However, these watches meant that an enormous amount of time was spent watching sites. Therefore the transfer of methods to other sites may be impractical. In order to assist land owners to estimate the amount of human disturbance on their land for use with SCARE I plan to establish the minimum adequate period that should be spent at sites to obtain the average disturbance rate.

It is possible that military training was not measured adequately. There were two plots that I did not have full access to and relied on military records for data at certain times. I also did not record disturbance occurring at night but this could have an equal impact on behaviour and plot use, and there may be additional impacts on foraging ability. Effects of military disturbance are hampered by poor data collection by the MoD on the training sites. The use of GPS on vehicles and troops should make it easy to track disturbance establish the most heavily used areas, but the information is not easily available for research.

The study was carried out entirely in the Wessex population of stone curlews, but there is no reason to suggest that the results are not transferable to Breckland. Furthermore, the results of this thesis are limited to stone curlews but it is thought that the methods can be applied to other species given the appropriate data collection.

9.7 Suggestions for further research

There are many issues which have arisen during this study which could not be covered in the thesis but which may be important to address in the future:

1. Establishing if there are any differences in responses to dogs on leads and off leads.
Given that most dogs were off leads, though under control, in this study, this may have to be achieved through further experiments.
2. The effect of larger group sizes of PDAs on stone curlew behaviour, plot use and breeding success. This may have to be tested through an experimental approach.
3. The effect of temporary military camps on SPTA, on desertion, breeding success and behaviour.
4. The further development of adequate predictive models of recreational disturbance event rate, including other possible correlates of disturbance.
5. Establishing if there are any differences in behavioural responses to disturbance by stone curlews on semi-natural chalk grassland and arable crops, compared to the plots used in this study;
6. Establishing if there are any differences between Wessex and Breckland stone curlews in their susceptibility to disturbance and behavioural responses;
7. Further analysis of habituation to disturbance.
8. Continued testing and improving of SCARE after feedback from users.
9. The inclusion of other variables into SCARE (for example proximity to roads or habitat variables) to improve predictive power without the need to collect data on PDA types and frequencies.
10. Collection of similar data and application of new methods of analysis of behavioural responses and resources use, for other potentially vulnerable species.

9.8 Conclusion

This thesis has provided evidence that human disturbance is affecting stone curlews in Wessex in terms of affecting behaviour and influencing nesting habitat use. New methods of measuring

disturbance have been developed and it is thought that these are robust enough to direct the management of access and placement of new plots with respect to disturbance. Furthermore, a tool has been developed to aid the delivery of the results, which should ensure correct implementation. As a result, access and military training may be adequately managed near stone curlew sites so that stone curlew conservation does not suffer. Thankfully, there is tremendous commitment from individuals and the RSPB, EN and DEFRA, who, working together, will help secure the future of stone curlews in Wessex and beyond.

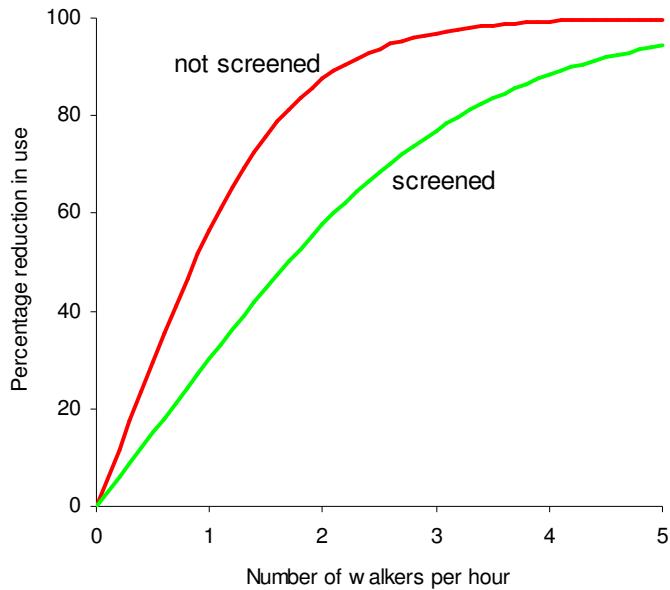


Figure 9.1. The output graph from SCARE. The graph shows the percentage by which the probability of plot occupancy would be reduced, compared with the probability with no disturbance, plotted against PDA event rate. This can be done with a specified mixture of PDA types, but the example is for one type. The lower line shows the effect of screening part of the route.

References

- Abrams, P.A. 1994. Should prey overestimate their risk of predation? *American Naturalist*, **144**, 317-328.
- Aebischer, N.J. 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study*, **46**, 22-31.
- Ahlund, M. and Gotmark, F. 1989. Gull predation on eider ducklings *Somateria mollissima*: Effects of human disturbance. *Biological Conservation*, **48**, 115-127.
- Amat, J.A. 1986. Information on the diet of the stone curlew *Burhinus oedicnemus* in Donana in Southern Spain. *Bird Study*, **44**, 71-73.
- Amat, J.A. and Masero, J.A. 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour*, **67**, 293-300.
- Amat, J.A., Fraga, R.M. and Arroyo, G.M. 2001. Intraclutch egg-size variation and offspring survival in the Kentish plover *Charadrius alexandrinus*. *Ibis*, **143**, 17-23.
- Andersen, D. E., Rongstad, O. J. and Mytton, W.R. 1990. Home-range changes in raptors exposed to increased human activity levels in southeastern Colorado. *Wildlife Society Bulletin*, **18**, 134 -142.
- Andersen, R., Linnell, J.D.C. and Langvatn, R., 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. *Biological Conservation*, **77**, 169-176.
- Anderson, D. W. 1988. Dose-response relationship between human disturbance and Brown Pelican breeding success. *Wildlife Society Bulletin*, **16**, 339 – 345.
- Anderson, D. W. and Keith, J. O. 1980. The human influence on sea bird nesting success: Conservation implications. *Biological Conservation*, **18**, 65 – 80.
- Arroyo, B. and Razin, M. 2006. Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees. *Biological Conservation*, **128**, 276-284.
- Atienza, J.C., Munoz, M. and Moral, J.C. 2001. Nesting habitat of black vultures *Aegypius monachus* and its implications for management. *4th Eurasian Congress on Raptors*, Seville, Spain.
- Augustin, N.H., Mugglestone, M.A. and Buckland, S.T., 1996. An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology*, **33**, 339-347.
- Badyaev, A.V., Martin, T.E. and Etges, W.J. 1996. Habitat sampling and habitat selection by female wild turkeys: ecological correlates and reproductive consequences. *Auk*, **113**, 636-646.
- Barash, D.P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. *Wilson Bulletin*, **87**, 367-373.
- Bathe, G. 2001. *Countryside and Rights of Way Act 2000. A user's guide*. Unpublished report, Peterborough, UK: English Nature.
- Batten, L.A., Bibby, C.J., Clement, P., Elliot, G.D. and Porter, R.F. 1990. *Red Data Birds in Britain*. Poyser, London.
- Beale, C.M., and Monaghan, P. 2004. Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, **41**, 335-343.
- Bealey, C.E., Green, R.E., Robson, R., Taylor, C.R. and Winspear, R. 1999. Factors affecting the numbers and breeding success of stone curlews *Burhinus oedicnemus* at Porton Down, Wiltshire. *Bird Study*, **41**, 68-75.
- Béchet, A., Giroux, J.-F. and Gauthier, G. 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. *Journal of Applied Ecology*, **41**, 689-700.
- Belanger, L. and Bedard, J. 1989. Responses of staging Greater Snow Geese to human disturbance. *Journal of Wildlife Management*, **53**, 713-719.
- Belanger, L. and Bedard, J. 1990. Energetic cost of man-induced disturbance to staging Snow Geese. *Journal of Wildlife Management*, **54**, 36-41.
- Benoit, M. P. and Bretagnolle, V. 2002. Seabirds of the southern Lagoon of New Caledonia; Distribution, abundance and threats. *Waterbirds*, **25**, 202-213.

- Berg, A., Lindberg, T. and Kallebrink, K.G. 1992. Hatching success of lapwings on farmland: differences between habitat and colonies of different sizes. *Journal of Animal Ecology*, **61**, 469-476.
- BirdLife International. 2004. *Birds in Europe: Population Estimates, Trends and Conservation*. Cambridge: BirdLife International.
- Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications*, **6**, 506-519.
- Blomqvist D. and Johansson, O.C. 1995. Tradeoffs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*. *Ibis*, **137**, 550-558.
- Blomqvist D., Johansson, O.C. and Gotmark, F. 1997. Parental quality and egg size affect chick survival in a precocial bird, the Lapwing *Vanellus vanellus*. *Oecologia*, **110**, 18-24.
- Bluhdorn, I. 1998. The impact of potential disturbances on the behaviour of Lapwings *Vanellus vanellus* during incubation and chick rearing. *Vogelwelt*, **119**, 105-113.
- Blumstein, D. T., Anthony, L. L., Harcourt, R. and Ross, G. 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation*, **110**, 97-100.
- Blumstein, D.T. 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, **71**, 389-399.
- Blumstein, D.T., Fernandez-Jurici, E., Zollner, P.A. and Garity, S.C. 2005. Interspecific variation in antipredator behaviour and human-wildlife coexistence. *Journal of Applied Ecology*, **42**, 943-953.
- Bolduc, F. and Guillemette, M., 2003. Human disturbance and nesting success of common eiders: interaction between visitors and gulls. *Biological Conservation*, **110**, 77-83.
- Bouskila, A. and Blumstein, D.T. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. *American Naturalist*, **139**, 161-176
- Boyd, J.C. and Sladen, J.L. 1971. Telemetry studies of the internal body temperature of Adelie and Emperor penguins at Cape Crozier, Ross Island, Antarctica, *Auk*, **88**, 366-380.
- Brown, W.S. 1993. Biology, status and management of the timber rattlesnake *Crotalus horridus*: a guide for conservation. *Society for the Study of Amphibians, Reptiles and Herpetology Circular*, **22**, 1-78.
- Burger, J. 1981. Effect of human activity on birds at a coastal bay. *Biological Conservation*, **21**, 231-241.
- Burger, J. 1986. The effect of human activity on shorebirds in two coastal bays in Northeastern United-States. *Environmental Conservation*, **13**, 123-130.
- Burger, J. 1991. Foraging behaviour and the effects of human disturbance on the piping plover *Chararius melanotos*. *Journal of Coastal Research*, **7**, 39.
- Burger, J. 1994. The effect of human disturbance on foraging behaviour and habitat use in piping plover *Chararius melanotos*. *Estuaries*, **17**, 695-701.
- Burger, J., Gochfeld, M. and Niles, L. J. 1995. Ecotourism and birds in coastal New Jersey – contrasting responses of birds, tourists, and managers. *Environmental Conservation*, **22**, 56.
- Burger, J. and Gochfield, M. 1991. Human disturbance and birds: tolerance and response distance of resident and migrant species in India. *Environmental Conservation*, **18**, 158-165.
- Burger, J. and Gochfield, M. 1993. Tourism and short term behavioural responses of nesting masked, red-footed and blue-footed boobies in the Galapagos. *Environmental Conservation*, **20**, 255-259.
- Burger, L. 1981. Effects of human disturbance on colonial species, particularly gulls. *Colonial Waterbirds*, **4**, 28-36.
- Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews*, **77**, 1-26.
- Caughley, G. 1994. Directions in Conservation biology. *Journal of Animal Ecology*, **63**, 215-244.
- Conomy, J.T., Dubovsky, J.A., Collazo, J.A. and Fleming, W.J. 1998. Do black ducks and wood ducks habituate to aircraft disturbance. *Journal of Wildlife Management*, **62**, 1135-1142.
- Cooke, A. S. 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biological Conservation*, **18**, 85-88.

- Cooper, W.E. 1997. Threat factors affecting antipredatory behaviour in the broad headed skink *Eumeces laticeps*: repeated approach, change in predator path and predator's field of view. *Copeia*, **1997**, 614-617.
- Cooper, W.E. 1998. Direction of predator turning, a neglected cue to predator risk. *Behaviour*, **135**, 55-64.
- Countryside Agency 2002. Access to the countryside (<http://www.countryside.gov.uk/access/>)
- Countryside Agency, 2002. New Rights, New Responsibilities. The Countryside Agency, leaflet CA 65.
- Cramp, S and Simmons, K.E.L. 1983. *The Birds of the Western Palearctic 3*. Oxford University Press, Oxford.
- Crawley, M.J. 2002. *Statistical Computing: An Introduction to Data Analysis using S-Plus*. John Wiley and Sons, Chichester.
- Cresswell, W. 1993. Escape responses by redshanks *Tringa totanus* on attack by avian predators. *Animal Behaviour*, **46**, 609-611.
- Cromack, R.M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika*, **54**, 429-238.
- Dawkins, R. and Carlisle, T.R. 1976. Parental investment: mate decision and a fallacy. *Nature*, **262**, 131-133.
- Day, T. C. F. 2003. *The effects of disturbance from roads on stone curlews in southern England*. Ph.D. thesis. University of Cambridge, Cambridge.
- Department for Environment, Food, and Rural Affairs (DEFRA). <http://www.defra.gov.uk/>. Accessed September 2006.
- de Villiers, M., Bause, M., Giese, M. and Fourie, A. 2006. Hardly hard-hearted: heart rate responses of incubating Northern Giant Petrels *Macronectes halli* to human disturbance on sub-Antarctic Marion Island. *Polar Biology*, **29**, 717-720.
- DeSanto, T.L. and Willson, M.F. 2001. Predator abundance and predation of artificial nests in natural and anthropogenic coniferous forest edges in SE Alaska. *Journal of Field Ornithology*, **72**, 136-149.
- Dill, L.M. 1974a. The escape response of the zebra danio *Brachydanio rerio*. I. The stimulus for escape. *Animal Behaviour*, **22**, 711-722.
- Dill, L.M. 1974b. The escape response of the zebra danio *Brachydanio rerio*. I. The effect of experience. *Animal Behaviour*, **22**, 723-730.
- Doligez, B., Part, T., and Danchin, E. 2004. Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection. *Animal Behaviour*, **67**, 457-466.
- Doligez, B, Danchin, E., and Clobert, J. 2002. Public Information and Breeding Habitat Selection in a Wild Bird Population. *Science*, **297**, 1168-1170.
- Donald, P.F., Evans, A.D., Muirhead, L.B., and Buckingham, D.L. 2002. Survival rates, causes of failure and productivity of skylark *Alauda arvensis* nests on lowland farmland. *Ibis*, **144**, 652-666.
- Donazar, J. A., Hiraldo, F. and Bustamante, J. 1993. Factors influencing nest site selection, breeding density and breeding success in the bearded vulture *Gypaetus barbatus*. *Journal of Applied Ecology*, **30**, 504-514.
- Dowling, B. and Weston, M. A. 1999. Managing a breeding population of the Hooded Plover *Thinornis rubricollis* in a high-use recreational environment. *Bird Conservation International*, **9**, 255-270.
- Eldridge, J.L. and Krapu, G.L. 1988. The influence of diet quality on clutch size and laying patterns in mallards. *Auk*, **105**, 102-110.
- Ellenberg, U., Mattern, T., Seddon, P.J. and Luna Jorquera, G. 2006. Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. *Biological Conservation*, **133**, 95-106.
- Ellis, M.E. 1982. Evolution of aversive information processing: A temporal tradeoff hypothesis. *Brain Behaviour and Evolution*, **21**, 151-160.
- Ens, B. J., Kersten, M., Brenninkmeijer, A. and Hulscher, J. B. 1992. Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **61**, 703-715
- Erwin, R., M. 1989. Responses to human intruders by birds nesting in colonies: experimental results and management guidelines. *Colonial Waterbirds*, **12**, 104-108
- Evans, D.M. and Day, K.R. 2002. Hunting disturbance on a shallow lake: the effectiveness of wildfowl refuges. *Ibis*, **144**, 2-8.

- Fairbanks, W.S. and Tullous, R. 2002. Distribution of Pronghorn on Antelope Island State Park, Utah, USA. *Natural Areas Journal*, **22**, 277-282.
- Fargallo, J.A., Blanco, G. and Soto-Largo, E. 1998. Forest management effects on nesting habitat selected by Eurasian black vultures *Aegypius monachus* in central Spain. *Journal of Raptor Research*, **32**, 202-207.
- Fernandez, C. and Azkona, P. 1993. Human disturbance effects on marsh harriers and nutritional status of nestlings. *Journal of Wildlife Management*, **57**, 602-608.
- Fernandez-Juricic, E. 2000. Local and regional effects of pedestrians on forest birds in a fragmented landscape. *The Condor*, **102**, 247-255.
- Fernandez-Juricic, E., and Telleria, J. L. 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study*, **47**, 13-21.
- Fernandez-Juricic, E., Jimenez, M. D. and Lucas, E. 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environmental Conservation*, **28**, 263-269.
- Fernandez-Juricic, E., Jimenez, M. D., and Lucas, E. 2002. Factors affecting intra- and inter-specific variations in the difference between alert and flight distances in forested habitats. *Canadian Journal of Zoology*, **80**, 1212-1220.
- Finney, S.K., Pearce-Higgins, J.W. and Yalden, D.W. 2004. The effect of recreational disturbance on two upland breeding birds the golden plover *Pluvialis apricaria* and the dunlin *Calidris alpina*. English Nature Research Report: Project Reference FST20-11-011.
- Finney, S.K., Pearce-Higgins, J.W., and Yalden, D.W. 2005. The effect of recreational disturbance on an upland breeding bird, the golden plover *Pluvialis apricaria*. *Biological Conservation*, **121**, 53-63.
- Fitzpatrick, S. and Bouchez, B. 1998. Effects of recreational disturbance on the foraging behaviour of waders on a rocky beach. *Bird Study*, **45**, 157-171.
- Fleming, S., Chiasson, R. D., Smith, P. C., Austin-Smith, P. J. and Bancroft, R. P. 1988. Piping plover status in Nova Scotia related to reproductive and behavioural responses to human disturbance. *Journal of Field Ornithology*, **59**, 321-330.
- Forsman, J.T., Monkkonen, M. and Hukkanen, E. 2001. Effects of predation on community assembly and spatial dispersion of breeding forest birds. *Ecology*, **82**, 232-244.
- Forstmeier W. and Weiss, I. 2004. Adaptive plasticity in nest site selection in response to changing predation risk. *Oikos*, **104**, 487-499.
- Fowler, G. S. 1999. Behavioural and hormonal responses of Magellanic penguins *Spheniscus magellanicus* to tourism and nest site visitation. *Biological Conservation*, **90**, 143-149.
- Fowler, G.S. 1993. Field studies, tourism and stress responses in Magellanic penguins. In: Fraser, W.R., Trivelpiece, W.Z (eds) Report: *Workshop on researcher-seabirds interactions*, Minnesota, Montana, USA: 44.
- Fowler, G.S. 1999. Behavioural and Hormonal responses of Magellanic penguins to tourism and nest site visitation. *Biological Conservation*, **90**, 143-149.
- Fox, A.D., Jones, T.A., Singleton R. and Agnew, A.D.Q. 1994. Food supply and effects of recreational disturbance on the abundance and distribution of wintering pochard on a gravel pit complex in southern Britain. *Hydrobiologia*, **279/280**, 253-261.
- Fraser, J.D., Frenzel, L. and Mathisen, J.E. 1985. The impact of human activities on breeding bald eagles in north-central Minnesota. *Journal of Wildlife Management*, **49**, 585-592.
- Frid, A. and Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11.
- Galbraith, H., 1988. Effects of agriculture on the breeding ecology of lapwings *Vanellus vanellus*. *Journal of Applied Ecology*, **25**, 487-503.
- Gavashelishvili, A. and McGrady, M.J. 2006. Breeding site selection by bearded vulture *Gypaetus barbatus* and Eurasian griffon *Gyps fulvus* in Caucasus. *Animal Conservation*, **9**, 159-170.
- Ghalambor, C.K. and Martin, T.E. 2001. Fecundity-survival trade-offs and parental risk taking in birds. *Science*, **292**, 494-497.
- Gibbons, D.W., Avery, M.I., Baillie, S.R., Gregory, R.D., Kirby, J., Porter, R.F., Tucker, G.M. and Williams, G. 1996. Bird species of conservation concern in the UK, Channel Islands and Isle of Man: revising the red data list. *RSPB Conservation Review*, **10**, 7-18.

- Giese, M. 1996. Effects of human activity on Adelie penguin *Pygoscelis adeliae* breeding success. *Biological Conservation*, **75**, 157-164.
- Gill, J. A. 1996. Habitat choice in wintering pink-footed geese: quantifying the constraints determining winter site use. *Journal of Applied Ecology*, **33**, 884-892.
- Gill, J.A. and Sutherland, W.J. 2000. Predicting the consequences of human disturbance from behavioural decisions. In: Gosling, L.M. and Sutherland, W.J. (eds) *Behaviour and Conservation*. Cambridge University Press, Cambridge, UK.
- Gill, J. A., Sutherland, W. J. and Watkinson, A. R. 1996. A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology*, **33**, 786-792.
- Gill, J.A., Norris, K. and Sutherland, W.J., 2001a. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**, 265-268.
- Gill, J.A., Norris, K. and Sutherland, W.J., 2001b. The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*. *Journal of Applied Ecology*, **38**, 846-856.
- Goldin, M.R. and Regosin, J.V. 1998. Chick behaviour, habitat use, and reproductive success of Piping Plovers at Goosewing Beach, Rhode Island. *Journal of Field Ornithology*, **69**, 228-234.
- Gonzalez, L.M., Arroyo, B.E., Margalida, A., Sanchez, R. and Oria, J. 2006. Effect of human activities on the behaviour of breeding Spanish imperial eagles *Aquila adalberti*: management implications for the conservation of a threatened species. *Animal Conservation*, **9**, 85-93.
- Goodrich, J.M., Berger, J., 1994. Winter recreation and hibernating black bears *Ursus americanus*. *Biological Conservation*, **67**, 105-110.
- Goss-Custard, J.D., Caldow, R. W. G., Clarke, R. T., Durell, S.E.A. Le V. dit, Urif, J., West, A. D. 1995. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis*, **137** (Suppl. 1), 56-66.
- Gotmark, F. 1992. The effects of investigator disturbance on nesting birds. *Current Ornithology* **9**, 63-104.
- Gotmark, F., Ahlund, M. 1984. Do field observers attract nest predators and influence nesting success of Common Eiders? *Journal of Wildlife Management*, **48**, 381-387.
- Gotmark, F., Blomqvist, D., Johansson, O.C. and Bergvist, J. 1995. Nest site selection: a trade off between concealment and view of surroundings? *Journal of Avian Biology*, **26**, 305-312.
- Gratto, C.L., Cooke, F. and Morrison, R.I.G. 1983. Nesting success of yearling and older breeders in the semipalmated sandpiper, *Calidris pusilla*. *Canadian Journal of Zoology*, **12**, 134-152.
- Green, R.E. 1984. Nomograms for estimating the stage of incubation of wader eggs in the field. *Wader Study Group Bulletin*, **42**, 36-39.
- Green, R.E. 1988. Stone curlew conservation. *RSPB Conservation Review*, **2**, 30-33.
- Green, R.E. and Griffiths, G.H. 1994. Use of preferred nesting habitat by Stone-curlews *Burhinus oedicnemus* in relation to vegetation structure. *Journal of Zoology*, **233**, 457-471.
- Green, R.E. 1995. Monitoring of Stone-curlew numbers and breeding success. In Carter, S.P. (ed.) *Britain's Birds in 1991-92: The Conservation and Monitoring Review*: 138-141. Thetford: British Trust for Ornithology and Joint Nature Conservation Committee.
- Green, R.E., and Bowden, C.G.R. 1986. Field characters for aging and sexing stone curlews. *British Birds*, **79**, 419-422.
- Green, R.E. and Taylor, C.R. 1995. Changes in stone curlew *Burhinus oedicnemus* distribution and abundance and vegetation height on chalk grassland at Porton Down, Wiltshire. *Bird Study*, **42**, 177-181.
- Green, R.E. and Tyler, G.A. 1989. Determination of the diet of the stone curlew by faecal analysis. *Journal of Zoology*, **217**, 311-320.
- Green, R.E., Hodson, D.P. and Holness, P.R. 1997. Survival and movements of stone curlews *Burhinus oedicnemus* ringed in England. *Ringing and Migration*, **18**, 102-112.

- Green, R.E., Tyler, G.A. and Bowden, C.G.R. 2000. Habitat selection, ranging behaviour and diet of the Stone-curlew *Burhinus oedicnemus* in southern England. *Journal of Zoology*, **250**, 161-183.
- Green, R.E., Ash, D. and Austin, M. 2002. Factors affecting the use of plots by stone curlews at Salisbury Plain Training Area and their breeding success. Unpublished report.
- Gregory, R. D., Wilkinson, N. I., Noble, D. G., Robinson, J. A., Brown, A. F., Hughes, J., Proctor, D. A., Gibbons, D. W. and Galbraith, C. A. 2002. The population status of birds in the United Kingdom, Channel Islands and the Isle of Man: an analysis of conservation concern 2002-2007. *British Birds*, **95**, 410-450.
- Grubb, T. G. and King, R. M. 1991. Assessing human disturbance of breeding bald eagles with classification tree models. *Journal of Wildlife Management*, **55**, 500-511.
- Grubb, T. G., Bowerman, W. W., Giesy, J. P. and Dawson, G. A. 1992. Responses of breeding bald eagles *Haliaeetus leucocephalus* to human activities in North central Michigan. *Canadian Field-Naturalist*, **106**, 443-453.
- Gutzwiller, K., Wiedenmann, R. T., Clements, K. L. and Anderson, S. H. 1994. Effects of human intrusion on song occurrence and singing consistency in subalpine birds. *Auk*, **111**, 28-37.
- Gutzwiller, K. J., Kroese, E. A., Anderson, S. H. and Wilkins, C. A. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? *Auk*, **144**, 55-65.
- Gutzwiller, K., Clements, K. L., Marcum, H. A., Wilkins, C. A. and Anderson, S. H. 1998 a???. Vertical distributions of breeding-season birds: is human intrusion influential? *Wilson Bulletin*, **110**, 497- 503.
- Gutzwiller, K., Marcum, H. A., Harvey, H. B., Roth, J. D. and Anderson, S. H. 1998b???. Bird tolerance to human intrusion in Wyoming montane forests. *Condor*, **100**, 519-527.
- Gutzwiller, K. J., Riffell, S. K., and Anderson, S. H. 2002. Repeated human intrusion and the potential for nest predation by gray jays. *Journal of Wildlife Management*, **66**, 372-380.
- Halfman, G. S. 1986. Behavioural responses of prey fishes during predator-prey interactions. In: M. E. Feder and G. V. Lauder (eds.), *Predator-prey relationships: Perspectives and approaches from the study of lower vertebrates*, pp. 135-156. University of Chicago Press, Chicago, Illinois.
- Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R. and Treweek, J. 1997 Bird disturbance: improving the quality and utility of disturbance research. *Journal of Applied Ecology*, **34**, 275-288.
- Hill, D.A. 1984. Laying date, clutch size and egg size of the mallard *Anas platyrhynchos* and tufted duck *Aythya fuligula*. *Ibis*, **126**, 484-495.
- Hipfner, J.M., Gaston, A.J. and de Forest, L.N. 1997. The role of female age in determining egg size and laying date of thick-billed murres. *Journal of Avian Biology*, **28**, 271-278.
- Hockin, D., Ounsted, M., Gorman, M., Hill, D., Keller, V. and Barker, M.A. 1992. Examination of the effects of disturbance on birds with reference to its importance in ecological assessments. *Journal of Environmental Management*, **36**, 253-286.
- Holloway, J. 1991. *The Historical Atlas of Breeding Birds in Britain and Ireland: 1875-1900*. Poyser, UK
- Holmes, N., Giese, M. and Kriwoken, L.K. 2005. Testing the minimum approach distance guidelines for incubating Royal penguins *Eudyptes schlegeli*. *Biological Conservation*, **126**, 339-350.
- Holmes, N.D., Giese, M., Achurch, H., Robinson, S. and Kriwoken, L.K. 2006. Behaviour and breeding success of gentoo penguins *Pygoscelis papua* in areas of low and high human activity. *Polar Biology*, **29**, 399-412.
- Holmes, T.L. Knight, R.L., Stegall, L. and Craig, G.R. 1993. Responses of wintering grassland raptors to human disturbance. *Wildlife Society Bulletin*, **21**, 461-468.
- Hunt, G.L. 1972. Influence if food distribution and human disturbance on the reproductive success of herring gulls. *Ecology*, **30**, 146-166.
- Huppop, O. 1995. Störungsbewertung anhand physiologischer Parameter. *Ornithologische Beobachter*, **92**, 257-268.
- Hüppop, O. and Gabrielsen, G. W. 1998 Energetic Consequences of human disturbances. In the Proceedings of the 22nd International Ornithological Congress. *Ostrich*, **69**, 171-172
- Hurley, A.C. and Hartline, P.H. 1974. Escape responses of the damselfish: a quantitative study. *Animal Behaviour*, **22**, 430-437.

- Hutson, G.D. 1982. Flight distance in Merino sheep. *Animal Production*, **35**, 231-235.
- Ikuta, L. A. and Blumstein, D. T. 2003. Do fences protect birds from human disturbance? *Biological Conservation*, **112**, 447-452.
- Janis, M.W. and Clark, J.D. 2002. Responses of Florida panthers to recreational deer and hog hunting. *Journal of Wildlife Management*, **66**, 839-848.
- Jokimaki, J. and Huhta, E. 2000. Artificial nest predation and abundance of birds along an urban gradient. *Condor*, **102**, 838-847.
- Keller, V. 1989. Variations in the response of great crested grebes *Podiceps cristatus* to human disturbance - a sign of adaptation. *Biological Conservation*, **49**, 31-45.
- Kenward, R.E. 1978. Hawks and Doves: Factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology*, **47**, 449-460.
- Kiltie, R.A. 2000. Scaling of visual acuity with body size in mammals and birds. *Functional Ecology*, **14**, 226-234.
- Kitchen, D.W. 1974. Social behaviour and ecology of the pronghorn. *Wildlife Monographs*, **38**, 1-96.
- Klein, M. L., Humphrey, S. R. and Percival, H. F. 1995. Effects of ecotourism on distribution of waterbirds in a wildlife refuge. *Conservation Biology*, **9**, 1454-1465.
- Knight, R.L. and Temple, S.A. 1986. Why does intensity of avian nest defence increase during the nesting cycle? *Auk*, **103**, 318-327.
- Koivula, K. and Ronka, A. 1998. Habitat deterioration and efficiency of antipredator strategy in a meadow-breeding wader, Temminck's Stint *Calidris temminckii*. *Oecologia*, **116**, 348-355.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- Lafferty, K. D. 2001. Birds at a Southern California beach: seasonality, habitat use and disturbance by human activity. *Biodiversity and Conservation*, **10**, 1949-1962.
- Lafferty, K. D. 2001. Disturbance to wintering western snowy plovers. *Biological Conservation*, **101**, 315-325.
- Liley, D., 1999. *Predicting the consequences of human disturbance, predation and sea-level rise for ringed-plover population size*. PhD Thesis, University of East Anglia, UK.
- Liley, D. 2001. *Access to the countryside and bird conservation: priorities for research*. Report for the Countryside Agency and English Nature, Peterborough, UK: English Nature.
- Liley, D., Jackson, D., and Underhill-Day, J. 2006. *Visitor access patterns on the Thames Basin Heaths*. English Nature Research Report.
- Lima, S.L. and Dill, L.M. 1990. Behavioural decisions made under the risk of predation. *Canadian Journal of Zoology*, **68**, 619-640.
- Lopez-Lopez, P., Garcia-Ripolles, C., Aguilar, J.M., Garcia-Lopez, F. and Verdejo, J. 2006. Modelling breeding habitat preferences of Bonelli's eagle *Hieraetus fasciatus* in relation to topography, disturbance, climate and land use at different spatial scales. *Journal of Ornithology*, **147**, 97-106.
- Lord, A., Waas, J.R. and Innes, J. 1997. Effects of human activity on the behaviour of northern New Zealand dotterel *Charadrius obscurus aquilonius* chicks. *Biological Conservation*, **82**, 15-20.
- Lord, A., Waas, J.R., Innes, J. and Whittingham, M.J. 2001. Effects of human approaches to nests of northern New Zealand dotterels. *Biological Conservation*, **98**, 233-240.
- Lunn, N.J., Stirlin, I., Andriashek, D. and Richardson, E. 2004. Selection of maternity dens by female polar bears in western Hudson Bay, Canada and the effects of human disturbance. *Polar Biology*, **27**, 350-356.
- MacIvor, L. H., Melvin, S. M. and Griffin, C. R. 1990. Effects of research activity on Piping Plover nest predation. *Journal of Wildlife Management*, **54**, 443-447.
- Madsen, J. 1985. Impact of disturbance on field utilization of Pink footed Geese in West Jutland, Denmark. *Biological Conservation*, **33**, 53-63.
- Madsen, J. 1995. Impacts of disturbance on migratory wildfowl. *Ibis*, **137**, S67-S74.

- Madsen, J. 1998. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. *Journal of Applied Ecology*, **35**, 398-417.
- Mallord, J.W. 2005. *Predicting the consequences of human disturbance, urbanisation and fragmentation for a woodlark Lullula arborea population*. Ph.D. thesis. University of East Anglia, Norwich.
- Marsden, S. J. 2000. Impact of disturbance on waterfowl wintering in a UK dockland redevelopment area. *Environmental Management*, **26**, 207-213.
- Martin, G.R. and Katzir, G. 1994. Visual-fields in the stone curlew *Burhinus oedicnemus*. *Ibis*, **136**, 448-453.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bulletin*, **87**, 456-466.
- McCraray M.D. and Pierson, M.O. 2000. Influence of human activity on shorebird use in Ventura County, California. *Proceedings of the Fifth Californian Islands Symposium*, 424-427.
- Meese, R.J. and Fuller, M. 1989. Distribution and behaviour of passerines around peregrine *Falco peregrinus* eyries of western Greenland. *Ibis*, **131**, 27-32.
- Miller, J.R. and Hobbs, N.T. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and Urban Planning*, **50**, 227-236.
- Miller, S. G., Knight, R. L. and Miller, C. K. 1998. Influence of recreational trials on breeding bird communities. *Ecological Applications*, **8**, 162-169.
- Miller, S. G., Knight, R. L. and Miller, C. K. 2001. Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin*, **29**, 124-132.
- Miller, S.G., Knight, R.L. and Miller, C.K. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications*, **8**, 162-169.
- Montgomrie, R.D. and Weatherhead, P.J. 1988. Risks and rewards of nest defense by parent birds. *The Quarterly Review of Biology*, **62**, 167-187.
- Moran-Lopez, R., Sanchez Guzman, J.M., Costillo Borrego, E. and Villegas Sanchez, A. 2006. Nest-site selection of endangered cinereous vulture *Aegypius monachus* populations affected by anthropogenic disturbance: present and future conservation implications. *Animal Conservation*, **9**, 29-37.
- Morris, D.W. 1987. Ecological scale and habitat use. *Ecology*, **68**, 362-369.
- MVA. 1999. *Access to other open countryside: measuring potential demand*. Unpublished report. English Nature, Peterborough, UK.
- Nager, R.G. and Zandt, H.S. 1994. Variation in egg size in great tits. *Ardea*, **82**, 315-328.
- Nethersole-Thompson, D. and Nethersole-Thompson, M., 1986. *Waders: Their breeding haunts and watchers*. A&AD Poyser, Calton, UK.
- Newton, I. 1998. *Population limitation in Birds*. Academic Press, London, UK.
- Nol, E., Brooks, R. J. 1982. Effect of predator enclosures on nesting success of killdeer. *Journal of Field Ornithology*, **53**, 263-268.
- Office of Public Sector Information (OPSI). <http://www.opsi.gov.uk/> Accessed September 2006.
- Ogilvie, F.M. 1920. *Field observations on British Birds*. London, Selwyn and Blount.
- Orians, G.H and Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. *American Naturalist*, **137**, S29-S49.
- Osborne, P.E., Alonso, J.C. and Bryant, R.G., 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology*, **38**, 458-471.
- Owens, N.W. 1977. Responses of wintering Brent Geese to Human Disturbance. *Wildfowl*, **28**, 5-14.
- Papouchis, C.M., Singer, F.J., Sloan, W.B., 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management*, **65**, 573-582.
- Parent, C. and Weatherhead, P.J. 2000. Behavioural and life history responses of eastern massasauga rattlesnakes *Sistrurus catenatus catenatus* to human disturbance. *Oecologia*, **125**, 170-178.

- Park, K.J., Robertson, P.A., Cambell, S.T., Foser, R., Russell, Z.M., Newborn, D. and Hudson, P.J. 2001. The role of invertebrates in the diet, growth and survival of red grouse *Lagopus lagopus scoticus* chicks. *Journal of Zoology*, **254**, 137-145.
- Parslow, J.L.F. 1973. *Breeding Birds of Britain and Ireland*. Poyser, Berkhamsted, UK.
- Pearce-Higgins, J. W. and Yalden, D. W. 1997. The effect of resurfacing the Pennine Way on recreational use of blanket bog in the Peak District National Park, England. *Biological Conservation*, **82**, 337- 343.
- Petit, L.J. and Petit, D.R. 1996. Factors governing habitat selection by Prothonotary warblers: field tests of the Fretwell-Lucas models. *Ecological Monographs*, **66**, 367-387.
- Pfister, C., Harrington, B. A. and Lavine, M. 1992. The impacts of human disturbance on shorebirds at a migration staging area. *Biological Conservation*, **60**, 115-126.
- Pienkowski, M. W. 1983. Habitat specialisation in breeding shorebirds: a defense strategy against egg-predation? *Wader Study Group Bulletin*, **39**, 50.
- Pienkowski, M. 1984. Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: nest predation as a possible factor limiting distribution and time of breeding. *Journal of the Zoological Society of London*, **202**, 83-114.
- Pienkowski, M. W. 1992. The impact of tourism on coastal breeding waders in western and southern Europe: an overview. *Wader Study Group Bulletin*, **68**, 92-96.
- Pienkowski, M. W. and Evans, P. R. 1982. Breeding behaviour, productivity and survival of colonial and non-colonial Shelducks *Tadorna tadorna*. *Ornis Scandinavica*, **13**, 101-116.
- Poirazidis, K., Goutner, V., Skartsi, T., and Stamou, G. 2004. Modelling nesting habitat as a conservation tool for the Eurasian black vulture *Aegypius monachus* in Dadia Nature Reserve, north-eastern Greece. *Biological Conservation*, **118**, 235-248.
- Potts, G.W. 1981. Behavioural interactions between the Carangidae (Pisces) and their prey on the fore-reef slope of Aldabra, with notes on other predators. *Journal of Zoology*, **195**, 385-404.
- Pulliam, H.R. 1973. On the advantages of flocking. *Journal of Theoretical Biology*, **38**, 419-422.
- Quinn, J.L. and Cresswell, W. 2004. Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology*, **73**, 143-154.
- Ramos, J.A. 2001. Seasonal variation in reproductive measures of tropical roseate terns *Sterna dougallii*: previously undescribed breeding patterns in a seabird. *Ibis*, **143**, 3-91.
- Ramsey, S.L. and Houston, D.C. 1997. Nutritional constraints on egg production in the blue tit: a supplementary feeding study. *Journal of Animal Ecology*, **66**, 649-657.
- Ratcliffe, D.A., 1976. Observations on the breeding of the golden plover in Great Britain. *Bird Study*, **23**, 63-116.
- Regal, J. and Putz, K. 1997. Effect of human disturbance on body temperature and energy expenditure in penguins. *Polar Biology*, **18**, 246-253.
- Richardson, C. T. and Miller, C. K. 1997. Recommendations for protecting raptors from human disturbance: a review. *Wildlife Society Bulletin*, **25**, 634-638.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology*, **9**, 1-48.
- Robertson, G.J. 1995. Annual variation in common eider egg size: Effects of temperature, clutch size, laying date and laying sequence. *Canadian Journal of Zoology*, **73**, 1579-1587.
- Robertson, G.J., Cooch, E.G., Lank, D.B., Rockwell, R.F. and Cooke, F. 1994. Female age and egg size in the lesser snow goose. *Journal of Avian Biology*, **25**, 149-155.
- Rodgers, J.A. and Smith, H.T. 1995. Set back distances to protect nesting bird colonies from human disturbance in Florida. *Conservation Biology*, **9**, 89-99.
- Rodgers, J. A, Smith, H. T. 1997. Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. *Wildlife Society Bulletin*, **25**, 139-145.
- Rodgers, J. A., Schwikert, S. T. 2002. Buffer-zone distances to protect foraging and loafing waterbirds from disturbance by personal watercraft and outboard-powered boats. *Conservation Biology*, **16**, 216-224.

- Ronconi, R.A. and Cassady St. Clair, C. 2002. Management options to reduce boat disturbance on foraging black guillemots *Cephus grylle* in the Bay of Fundy. *Biological Conservation*, **108**, 265-271.
- Roos, S. and Part, T. 2004. Nest predators affect spatial dynamics of breeding red-backed shrikes *Lanius collurio*. *Journal of Animal Ecology*, **73**, 117-127.
- Ruhlen, T.D., Abbott, S., Stenzel, L.E. and Page, G.W. 2003. Evidence that human disturbance reduces snowy plover chick survival. *Journal of Field Ornithology*, **74**, 300-304.
- Scaife, M. 1976. The response to eye-like shapes by birds II: The importance of staring pairness, and shape. *Animal Behaviour*, **24**, 200-206.
- Schauer, J. H. S. and Murphy, E. C. 1996. Predation on eggs and nestlings of Common Murres *Uria aalge* at Buff, Alaska. *Colonial Waterbirds*, **19**, 186-198.
- Schulz, R. and Stock, M. 1993. Kentish Plovers and tourists: competitors on sandy coasts? *Wader Study Group Bulletin*, **68**, 83-91.
- Sergio, F., Marchesi, L. and Pedrini, P. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology*, **72**, 232-245.
- Seymour, A.S., Harris, S., Ralston, C. and White, P.C.L. 2003. Factors influencing the nesting success of lapwings *Vanellus vanellus* and behaviour of red fox *Vulpes vulpes* in lapwing nesting sites. *Bird Study*, **50**, 39-46.
- Sharrock, J.T.R. 1976. *The Atlas of Breeding Birds in Britain and Ireland*. Tring: British Trust for Ornithology.
- Sidaway, R. 1990. *Birds and Walkers: a review of existing research on access to the countryside and disturbance to birds*. Ramblers Association, London.
- Sieving K.E. 1992. Nest predation and differential insular extinction among selected forest birds of Central Panama. *Ecology*, **73**, 2310-2328.
- Sillman, R.A. and Brown, A.F., 1994. Population sizes and habitat associations of upland breeding birds in the South Pennines, England. *Biological Conservation*, **69**, 307-314.
- Skagen, S. K., Knight, R. L. and Orians, G. H. 1991. Human disturbance of an avian scavenging guild. *Ecological Applications*, **1**, 215-225.
- Sockman, K. W. 1997. Variation in life-history traits and nest-site selection affects risk of predation in the Californian Gnatcatcher. *Auk*, **114**, 324-332.
- Sockman, K.W. 1997. Seasonal variation in nest placement by the California gnatcatcher. *Wilson Bulletin*, **112**, 498-504.
- Stalmaster, M. V., Kaiser, J. L. 1998. Effects of recreational activity on wintering bald eagles. *Wildlife Monographs* **137**, 1-46.
- Stalmaster, M.V. and Newman, J.R. 1978. Behavioural responses of wintering bald eagles to human intrusion. *Journal of Wildlife Management*, **42**, 506-513.
- Stamps, J.A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In: *Dispersal* (Ed. By J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols), pp. 230-242, Oxford University Press, Oxford.
- Stevens, M.A. and Boness, D.J. 2003. Influences of habitat features and human disturbance on the use of breeding sites by a declining population of southern fur seals *Arctocephalus australis*. *Journal of Zoology*, **260**, 145-152.
- Stienien, E.W.M. and Brenninkmeijer, A. 2002. Variation in growth in sandwich tern chicks *Sterna sandvicensis* and the consequences for pre- and post-fledging mortality. *Ibis*, **144**, 567-576.
- Stillman, R.A. and Goss-Custard, J.D., 2002a????. Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. *Journal of Avian Biology*, **33**, 358-365.
- Stillman, R. A. and Goss-Custard, J. D. 2002b????. Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. *Journals of Avian Biology*, **33**, 358-365.
- Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S.E.A. Le V. dit, Caldlow, R. W. G., McGrorty, S. and Clarke, R. T. 2000. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *Journal of Applied Ecology*, **37**, 564-588.
- Strauss, E. G. 1990. *Reproductive success, life history patterns and behavioural variation in a population of Piping Plover subjected to human disturbance*. PhD Thesis, Tufts University, U.S.A.

- Strauss, E. and Dane, B. 1989. Differential reproductive success in a stressed population of Piping Plovers in areas of high and low human disturbance. *American Zoologist*, **29**, 42.
- Stroud, D.A., Reed, T.M. and Harding, N.J., 1990. Do moorland breeding waders avoid plantation edges? *Bird Study*, **37**, 177-186.
- Sutherland, W.J. and Crockford, N.J. 1993. Factors affecting the feeding distribution of red-breasted geese *Branta ruficollis* wintering in Romania. *Biological Conservation*, **63**, 61-65.
- Sutherland, W.J. and Norris, K. 2002. Behavioural models of population growth rates: implications for conservation and predictions. *Philosophical Transactions of the Royal Society of London Series B*, **357**, 1273-1284.
- Sydeman, W.J. and Emslie, S.D. Effects of parental age on hatching asynchrony, egg size and third-chick disadvantage in western gulls. *Auk*, **109**, 242-248.
- Taylor, E. 2002. *Predation risk in woodlark Lullula arborea: the influence of recreational disturbance, predator abundance, nest site characteristics and temporal factors*. MSc. University of East Anglia, Norwich.
- Telesco, D.J. and Van Mamen, F.T. 2006. Do black bears respond to military weapons training? *Journal of Wildlife Management*, **70**, 222-230.
- Thomas, K., Kvitek, R.G. and Bretz, C., 2003. Effects of human activity on the foraging behaviour of sanderlings *Calidris alba*. *Biological Conservation*, **109**, 67-71.
- Thomson, R.L., Forsman, J.T., Sarda-Palomera, F. and Monkkonen, M. 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. *Ecography*, **29**, 507-514.
- Tucker, G. and Heath, A.F. 1994. *Birds in Europe: Their Conservation Status*. Cambridge: Birdlife International.
- Tuite, C. H., Hanson, P. R. and Owen, M. 1984. Some ecological factors affecting winter wildfowl distribution on inland waters in England and Wales, and the influence of water-based recreation. *Journal of Applied Ecology*, **21**, 41-62.
- Tuite, C. H., Owen, M. and Paynter, D. 1983. Interaction between wildfowl and recreation at Llangorse Lake and Talybont Reservoir, South Wales. *Wildfowl*, **34**, 48-63.
- Tulp, I. 1998. Nest success of white-fronted plover *Charadrius marginatus* and Kittlitz's plover *Charadrius pecuarius* in a South African dune field. *Wader Study Group Bulletin*, **87**, 51-54.
- Tydemar, C. F. 1977. The importance of the close fishing season to breeding bird communities. *Journal of Environmental Management*, **5**, 289-296.
- UK Biodiversity Action Plan. <http://www.ukbap.org.uk/ukplans>. Accessed September 2006.
- Underhill, M. C., Kirby, J. S., Bell, M. C. and Robinthwaite, J. 1993. *Use of waterbodies in southwest London by waterfowl. An investigation of the factors affecting distribution, abundance and community structure*. Report to Thames Water Utilities Ltd and English Nature. Wetlands Advisory service, Slimbridge. August 1993.
- Underhill, M., Pettifor, R. and Quinn, J. 1995. *A survey of the reaction by waterfowl in the inner Moray Firth to human recreational activities*. Wetlands Advisory Service, Draft Report August 1995.
- Urifi, A. J., Goss-Custard, J. D. and Durell, S. E. A. Le V. dit. 1996. The ability of oystercatchers *Haematopus ostralegus* to compensate for lost feeding time: field studies on individually marked birds. *Journal of Applied Ecology*, **33**, 873-883.
- Valkama, J., Robertson, P., and Currie, D. 1998. Habitat selection by breeding curlews *Numenius arquata* on farmland: the importance of grassland. *Annales Zoologici Fennici*, **35**, 141-148.
- van der Zande, Berkhuizen, J. C., van Latesteijn, H. C., ter Kurs, W. J. and Poppelaars, A. J. 1984. Impact of outdoor recreation on the density of a number of breeding bird species in woods adjacent to urban residential areas. *Biological Conservation*, **30**, 1-39.
- Verboven, N., Ens, B. J. and Dechesne, S. 2001. Effect of investigator disturbance on nest attendance and egg predation in Eurasian oystercatchers. *Auk*, **118**, 503-508.
- Verhulst, S., Oosterbeek, K. and Ens, B.J., 2001. Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. *Biological Conservation*, **101**, 375-380.
- Vos, D.K., Ryder, R.A. and Grand, W.D. 1985. Response of breeding Great Blue Herons to human disturbance in northcentral Colorado. *Colonial Waterbirds*, **8**, 13-22.

- Wallander, J., Isaksson, D. and Lenberg, T. 2006. Wader nest distribution and predation in relation to man-made structures on coastal pastures. *Biological Conservation*, **132**, 343-350.
- Walpole-Bond, J. 1938. *A History of Sussex Birds*. HF and G Witherby Ltd., London.
- Walther, F.R. 1969. Flight behaviour and avoidance of predators in Thomson's gazelle *Gazella thomsoni*. *Behaviour*, **34**, 184-221.
- Warren, C., 2000. Birds, bogs and forestry revisited: The significance of the Flow Country controversy. *Scottish Geographical Journal*, **116**, 315-337.
- Webb, P.W. 1981. Responses of northern anchovy larvae to predation by a biting planktivore. *Fish Bulletin of the United States*, **79**, 727-735.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: Age specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos*, **64**, 464-473.
- Weimerskirch, H., Shaffer, S. A., Mabille, G., Martin, J., Boutard, O. and Rouanet, J. L. 2002. Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effects of human disturbance. *Journal of Experimental Biology*, **205**, 475-483.
- West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W.G., Durell, S.E.A., Le V. dit and McGrorty, S. 2002. Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. *Biological Conservation*, **106**, 319-328.
- Whittingham, M. J., Percival, S. M. and Brown, A. F., 2000. Notes on night-time activity of golden plover *Pluvialis apricaria* chicks in the North Pennines. *Wader Study Group Bulletin*, **90**, 56-58.
- Whittingham, M.J., Percival, S.M., and Brown, A.F., 2001. Habitat selection by golden plover *Pluvialis apricaria* chicks. *Basic and Applied Ecology*, **2**, 177-191.
- Whittingham, M.J., Percival, S.M. and Brown, A.F., 2002. Nest-site selection by golden plover: why do shorebirds avoid nesting on slopes? *Journal of Avian Biology*, **33**, 184-191.
- Wiens, J.A. 1976. Population responses to patchy environment. *Annual Review of Ecology and Systematics*, **7**, 81-120.
- Williams, T.D. and Cooch, E.G. 1996. Egg size, temperature and laying sequence: why do snow geese lay big eggs when it's cold? *Functional Ecology*, **10**, 112-118.
- Woodfield, E, Langston, R. 2004. *A study of the effects on breeding nightjars of access on foot to heathland*. English Nature Research Report. English Nature, Peterborough.
- Wynde, R.M. 2006. Stone-curlews soar to new heights. *Birds*. **21**, 87.
- Yalden, D. W. 1986. The status of Golden Plover in the Peak District in relation to access and recreational disturbance. *Wader Study Group Bulletin*, **46**, 34-35.
- Yalden, D.W. 1990. Recreational disturbance of large mammals in the Peak District. *Journal of Zoology*, **221**, 293-296.
- Yalden, D. W. 1992. The influence of recreational disturbance on Common Sandpipers *Actitis hypoleucus* breeding by an upland reservoir, in England. *Biological Conservation*, **61**, 41-49.
- Yalden, D. W. and Pierce-Higgins, J. W. 1997. Density-dependence and winter weather as factors affecting the size of a population of golden plovers *Pluvialis apricaria*. *Bird Study*, **44**, 227-234.
- Yalden, D.W. and Yalden, P.E., 1988. The level of recreational pressure on blanket bog in the Peak District National Park, England. *Biological Conservation*, **44**, 213-227.
- Yalden, D. W. and Yalden, P. E. 1989. The sensitivity of breeding Golden Plovers *Pluvialis apricaria* to human intruders. *Bird Study*, **36**, 49-55.
- Yalden, P. E. and Yalden, D. W. 1990. Recreational disturbance of breeding Golden Plovers *Pluvialis apricaria*. *Biological Conservation*, **51**, 243-262.
- Yasue, M. 2006. Environmental factors and spatial scale influence shorebirds' responses to human disturbance. *Biological Conservation*, **128**, 47-54.
- Yasue, M. and Dearden, P. 2006. The effects of heat stress, predation risk and parental investment on Malaysian plover nest return times following a human disturbance. *Biological Conservation*, **132**, 472-480.

- Yasue, M. and Dearden, P. 2006. The potential impact of tourism development on habitat availability and productivity of Malaysian plovers *Charadrius peronii*. *Journal of Applied Ecology*, **43**, 978-989.
- Ydenberg, R.C. 1984. Great tits and giving up times: Decision rules for leaving patches. *Behaviour*, **90**, 1-24.
- Ydenberg, R.C. and Dill, L.M. 1986. The economics of fleeing for predators. *Advances in the Study of Behaviour*, **16**, 229-249.
- Yorio, P., Frere, E., Gandini, P. and Schiavini, A. 2001. Tourism and recreation at seabird breeding sites in Patagonia, Argentina: current concerns and future prospects. *Bird Conservation International*, **11**, 231-245.