

Nest survival and productivity of the critically endangered Sociable Lapwing *Vanellus gregarius*

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The Sociable Lapwing *Vanellus gregarius* is a critically endangered species, probably declining from 5000 pairs to 500 pairs in 11 years. Fieldwork was conducted at two sites in Kazakhstan, May–August 2004, to identify causes of the species' decline. In total, 58 nests and a minimum of 36 broods in 16 colonies were found: colonies consisted of 1–8 nests that were on average 154 m apart, with 2.1 km between colonies. Although classified as biparental, the total proportion of time both parents spent incubating was low ($77 \pm 2\%$ se, $n = 13$ nests). Daily survival rates (Mayfield method) were very low during incubation (0.943 ± 0.009 se) but high during the chick stage (0.986 ± 0.004 se); incubation and chick-stage durations were found to be 28.5 and 29 days, respectively, so that the overall probability of any breeding attempt fledging chicks was 0.124 (0.055–0.274 95% confidence interval). A breeding attempt that produced fledglings, fledged 2.2 ± 0.2 se chicks ($n = 26$) on average. Observed productivity predicted the population decline over the last 11 years well (using the maximum number of nesting attempts per pair of 1.4 that could have occurred in this study, and assuming an adult and first-year survival rate of 0.74 and 0.60, respectively, based on the means for Northern Lapwing *Vanellus vanellus* and Golden Plover *Pluvialis apricalia*). Nest survival during incubation (controlling for colony effects) may have been longer for nests in predominantly *Artemisia* rather than grass habitat. Mean nest survival for a colony was higher in areas with more bare ground and more nest predators, suggesting that predators were relatively unimportant in nest (egg or chick) mortality, but was lower in areas with high numbers of cattle, suggesting that trampling was important (64% of known-cause nest failures, $n = 11$, were trampled). Nests were preferentially sited in areas of *Artemisia*, where there was greater dung abundance, and probably shorter vegetation, suggesting that highly grazed vegetation is important for nesting. Chicks preferentially selected areas with a lower percentage of bare ground and possibly taller vegetation, suggesting that more vegetated areas are important for chicks. The results suggest that low egg survival due to nesting in areas of high grazer density may be responsible for the Sociable Lapwing's decline. Although grazers may create suitable vegetation for initial nesting, if those grazers remain at high density as in anthropogenic systems then they may reduce nest survival, probably through trampling. Experimentally maintaining grazing early but reducing it later in the breeding season is the logical first step in managing the species to increase egg survival and so to increase productivity.

The Sociable Lapwing *Vanellus gregarius* is a globally threatened species, classified as 'Vulnerable' (BirdLife

International 2000) until 2004, when it was reclassified (BirdLife International 2001) as 'Critically Endangered' by BirdLife International on the basis of its continued rapid population decline (Eichhorn & Heinicke 2000, Khrokov & Buketov 2000). The

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current breeding world population may be as low as 200 pairs, having declined from an estimated 2500–10 000 pairs in the last 15 years (BirdLife International 2002), and is now restricted to the steppes of Kazakhstan and narrow fringing regions of Russia. The districts of Naurzum (Kostanajskaya region) and Korgalzhyn (Akmolinskaya region) are well known as key breeding areas and many of the data accumulated on Sociable Lapwing in Kazakhstan originate from these sites (Khrokov 1977, 1996, Gordienko 1991). However, intensive breeding surveys in Naurzum reserve and adjacent areas, and in Korgalzhyn district, over the last 10 years have revealed an ongoing severe decline (Khrokov & Buketov 2000, Eichhorn & Khrokov 2002).

The reasons for this decline are unknown. Possible causes are a decline in productivity as a result of increased nest trampling rates, nest predation rates and human disturbance, all as a likely consequence of changes in agricultural practices (Gordienko 1991), and nesting habitat becoming more intensively grazed areas due to climatic and social change (Shevchenko 1998). Although factors on their migration routes and wintering grounds may be contributing to the decline, Sociable Lapwings winter in widely available habitat over a large area, are legally protected in most areas and have not been reported to be hunted (BirdLife International 2002). The recent international action plan for the Sociable Lapwing developed for the African Eurasian Waterbirds Agreement (AEWA) (BirdLife International 2002) concluded that urgent action was needed to determine the main factors negatively affecting the species' population in the breeding, migration and wintering areas. Clearly, if any effective conservation management to address the decline is to occur, an intensive research programme is needed to determine the breeding success and its importance in the population decline of the species. This study aimed partly to meet this objective by investigating the factors determining breeding productivity and its potential influence in the observed population decline.

METHODS

Fieldwork was carried out from May to August 2004 from breeding areas east of Lake Tengiz near Korgalzhyn (50°35'N, 70°01'E), central Kazakhstan. There were two main study sites, the villages of Korgalzhyn and Aktubek, located c. 150 km southwest from Astana, the capital city of Kazakhstan, and separated by 80 km from each other. Nests and

broods were located by observations of displaying birds and by cold-searching areas where nests and broods had been found in previous years as well as areas of apparently suitable habitat adjacent to previously known breeding areas. A team of fieldworkers was split into two units monitoring 44 nests in ten colonies around Korgalzhyn and 16 nests in six colonies around the villages of Shalkar, Aktubek and Kulanutpes. Additional trips were made to search for nests and broods at several other villages up to 50 km from Korgalzhyn. Some non-breeding flocks were seen at some of these other villages, and chicks from a single brood were ringed at Zhumay on 23 June. When a nest was located, its exact location was recorded on a GPS (Garmin e-trex): distances between nests and between colonies were then determined using the GOTO function.

Twenty-one adult Sociable Lapwings were caught on the nest following clutch completion and were colour-ringed for individual identification: all birds were caught with simple chicken-wire mesh walk-in traps placed over the nest and eggs at least 10 days after clutch completion. All resumed incubation shortly after release. Ninety-four chicks were also captured and fitted with colour rings for individual identification: no adverse effects on chicks owing to capture and ringing were observed. The birds were marked with four coloured plastic rings above the tibio-tarsal joint according to standard protocols for waders (Redfern & Clark 2001).

Nest and chick phenology and productivity

Nests were visited every 1–3 days. Initial visits involved 5–10 min spent at the nest to measure eggs, but later visits involved a brief visual check using a telescope from a sufficient distance to confirm the nest's continued survival (based on the presence of an incubating bird) without flushing the incubating bird. On one occasion a nest was believed to have failed immediately after a visit due to a dog following a fieldworker, but otherwise no obvious adverse effects of monitoring were noted. Nest age was determined by direct observation of the first day that a full clutch was present ($n = 8$), and then using egg measurements from these nests of known age, spread throughout the incubation period, to establish the relationship between egg density and time since clutch completion. Egg density was calculated as (mean egg {mass/[(width × width) × length]}) measured using dial callipers (to 0.1 mm) and a portable electronic

balance (to 0.01 g). Where the age of eggs was unknown they were measured in the same way, and their age estimated by using the regression relationship derived from nests of known age.

The incubation period was estimated for each nest from the observed hatch date to either the observed or the estimated (from egg density) date of first egg laid. The fledging period was estimated from chick growth curves. Individually colour-ringed chicks (therefore of known age and identity) were captured opportunistically and their mean mass measured using a 300-g Pesola balance (to 1 g). A sigmoid function of best fit was fitted to the mean of all mean brood measurements for each age (to the nearest day), and the point at which the asymptote was reached was considered to be the point of fledging. This coincided with observations of chicks at this age being able to fly and to act independently of their parents. The number of chicks still alive at the point of fledging, if greater than zero, was then recorded as a measure of chick production from successful breeding attempts. The number of breeding attempts per pair was estimated as the maximum possible from the distribution of clutch completion dates (see Fig. 3), assuming that all pairs that failed before the date at which a new attempt could have started did attempt to breed again (see Results).

Nest attendance

Nest attendance was measured using a flexibly tipped temperature probe (to 0.1 °C) connected to a TinyTag datalogger. The probe was placed in the centre of the clutch, and nest temperature was recorded every minute. As nest temperatures were above 35 °C while the female was incubating the clutch but air temperature rarely exceeded 30 °C, nest temperature changed when a bird departed from or returned to the nest; thus, the temperature traces provided a reasonably clear record of attendance that was accurate to the nearest minute (see Cresswell *et al.* 2004). The times that a bird departed from and returned to each nest were then used to calculate the duration of each incubation bout and each trip off the nest ($n = 19$ nests sampled). The total experimental sampling period for 13 nests was 24.2 ± 0.1 h so that any effects in attendance sampling due to diurnal variation in attendance were the same in all samples, and so these 13 nests were used to determine mean nest attendance (the sum of the total time spent incubating divided by the total sampling period).

Nest and chick survival

Daily nest survival probability was calculated using the standard Mayfield method (Mayfield 1961), with confidence intervals calculated according to Johnson (1979). The number of days that a breeding attempt survived during the nest stage was calculated as hatch or failure date minus first egg date, and the number of days that a breeding attempt survived during the chick stage was calculated as fledge or failure date minus hatch date.

A nest was considered to have failed if an incubating bird was not present on several successive visits, or if all eggs were missing or damaged. Causes of nest failure were determined where possible by observation of the condition of the nest or eggs. Hoof marks and destruction of the nest were classified as failure by trampling, eggs with puncture marks consistent with bill penetration were classified as failure by avian predators, nests dug out and destroyed completely were classified as failure by mammals (including dogs) and nests where eggs remained intact were classified as desertions. Where a nest had a TinyTag temperature probe, the time of failure was also used as evidence (e.g. nocturnal failure was probably caused by a mammal). A brood was considered to have failed if chicks could not be relocated after at least two successive visits to the immediate area, and after an extensive search of a larger area (1–2 km radius) around where it had previously been present, or if the colour-ringed adult was seen alone in circumstances that suggested that it had lost its chicks (absence of chick protection behaviour or vigilance, and having moved to an area well away from where its brood was last seen).

An index of trampling intensity and nest predator abundance was estimated for colonies by carrying out timed watches of 2 h in both morning and afternoon periods (17 May to 17 June) at each of 14 colonies (logistical reasons prevented these watches from being carried out at the remaining two colonies). An average of 5.6 ± 0.4 (se) watches were carried out per colony. During the watch the total numbers of potential predators of nests (gulls and corvids) and adults (raptors such as harriers), dogs, people and cattle or similar large grazers (horses, sheep and goats) passing through or over the colony were recorded. As the numbers of people ($r_s = 0.69$, $P = 0.006$, $n = 14$) and of dogs ($r_s = 0.69$, $P = 0.006$, $n = 14$) were highly correlated with the number of cattle, only the number of cattle was used for further analysis as trampling was suspected to be a major cause of

nest failure, and statistical power was limited in the model (i.e. only 14 colonies).

Nest and brood habitat selection

The following habitat variables were recorded for each nest on discovery and after the nest failed or after hatch at 1 m (one sample around the nest) and random samples at 10 m ($3 \times 1 \text{ m}^2$, 1 m apart at a random compass bearing from the nest), 100 m (three samples as at 10 m) and 500 m (three samples as at 10 m):

- (1) the maximum height of the vegetation (to 1 cm);
- (2) the dominant vegetation type (*Artemisia*, grass or moss);
- (3) the proportion of bare ground;
- (4) the proportion of ground covered by dung;
- (5) the distance to nearest water (to 10 m); and
- (6) the distance to nearest village (to 10 m, nest sample only).

The same habitat variables were recorded each time a brood was sighted.

Little variation in any variable was found between random samples at 10 m and 100 m (maximum t -value = 0.9) and so samples taken at 100 m were ignored in further analysis. Habitat variables varied more between 10 and 500 m (see Table 4 and Results), but there was most difference between the nesting habitat and available habitat at the 500-m scale (see Results) and so habitat selection analyses were carried out at the 500-m scale for both nests and broods.

There was significant variation in some habitat variables between the first sample at the nest on nest discovery and the sample at the nest after failure or hatch. Vegetation height decreased significantly (6.0 ± 0.4 during vs. 5.2 ± 0.3 cm after, $t = 2.6$, $P = 0.011$), and percentage bare ground increased significantly (58.8 ± 3.0 during vs. $64.0 \pm 3.0\%$ after, $t = -2.4$, $P = 0.017$). There was no significant change in percentage dung cover ($t = 1.5$, $P = 0.13$) and dominant vegetation type was exactly the same. Owing to this variation, habitat selection analyses were carried out by only comparing samples collected concurrently, after a nest had failed or hatched. Because there was a high degree of correlation between samples collected during and after nest occupation for all variables measured (minimum Pearson $R = 0.51$, $P < 0.001$), the change in vegetation during the nesting period should only greatly affect the absolute values of the variables, not their relative values, thereby making the habitat selection analyses (e.g.

whether nests were sited in shorter or longer vegetation relative to random points) meaningful.

Analysis

The analysis was structured to determine the basic breeding characteristics of the Sociable Lapwing that would determine the unit of statistical analysis and conservation management (nest or colony level) and the calculation of productivity measures. These included calculations of:

- (1) spacing between nests and between colonies;
- (2) proportion of attendance to confirm breeding system (biparental or uniparental);
- (3) daily survival rates during the incubation (pdsi) and the brood stage (pdsb);
- (4) the duration of the incubation period (di) – including clutch size;
- (5) the duration of the brood period (db);
- (6) the number of breeding attempts per pair per year (nba); and
- (7) the number of chicks produced per successful breeding attempt (c).

The observed productivity on the breeding ground was then used to model population change to determine whether it predicts the decline in Sociable Lapwing population. This was done in the simplest way by determining whether the chick output per pair per year matched the decrease in population as a result of first-winter and adult mortality. We therefore used the measures above to calculate annual productivity per pair:

- (8) overall chance that each nest and brood survives to fledge chicks (pns), $pns = pdsi^{(di)} \times pdsb^{(db)}$;
- (9) the number of chicks produced per pair per year (ncpp), $ncpp = pns \times c \times nba$.

We then used estimates of adult and first-winter survival to predict the number of birds that would die between breeding periods. As this study is only based on a single year, these estimates were not yet available for the Sociable Lapwing. We therefore used the best available estimates from similar species (see Sandercock 2003). We calculated the difference between the number of deaths and the number of first-year birds recruited each year and used this difference to plot the yearly change in population from the starting population estimate of 5000 pairs in 1989. We then compared whether our predicted population change resulted in the observed estimated population estimates in 2000 and 2002. The sensitivity of our predictions to our estimates of re-nesting rate, and of adult and first-year survival,

was also explored by varying these values in the model and observing their effects on the population change prediction.

Next, we determined which factors were influencing the chance that a nesting attempt was successful (i.e. nest or chick survival). The dependent variable in these analyses was the number of days survived from the start of the stage until the end of the stage or failure: note that this is not nest exposure, which is the number of days from discovery of the nest or brood until the end of the stage or failure. The number of days survived from the start of the stage was used in preference to exposure as the former is more accurate, measuring the exact number of days survived, and should not typically introduce bias that would result in increasing the probability of a Type I error. Although more nests will have been found with a greater survival probability (because these are available longer on average to be found), as long as some nests were found with lower survival probability (and many were) a regression-type analysis will not be greatly affected by their being fewer samples for nests with low survival probability. Any effects should act to make tests for significant correlates of nest survival more conservative (i.e. result in a Type II error). Nevertheless, we then checked the models produced by replacing the number of days survived from the start of the stage as dependent variable with nest exposure days according to the more conventional (but more conservative) logistic regression method of analysis of nest survival (Aebischer 1999, Hazler 2004).

First we used general linear models (GLMs) to determine whether egg-stage nest survival from clutch completion was correlated with the mean of habitat measurements collected per nest (dominant vegetation type, vegetation height, proportion of dung cover, proportion of bare ground cover, distance to nearest water and distance to nearest village). The analysis included clutch initiation date to control for seasonal effects, and colony was entered as a random factor to control for clustering of nests within colonies. Variables at $P \geq 0.15$ were then removed from the models and a minimum adequate model was obtained. The best model was then checked using a Mayfield logistic regression (Hazler 2004): whether nest stage succeeded or failed/number of exposure days was then substituted as the dependent variable and a binomial logistic regression carried out.

Secondly, we used GLMs to test whether the mean number of days of nest survival per colony was dependent on the index of cattle abundance, the

index of nest predator abundance and/or the index of adult predator abundance, controlling for habitat variables (mean proportion bare ground, dominant vegetation type and mean vegetation height) and season (mean clutch completion date). Variables at $P \geq 0.15$ were then removed from the models and a minimum adequate model was obtained. Distance to village and water were not included in the model because of limited power, but addition of these terms to the minimum adequate model decreases the predictive power of the model. The dependent variable was the mean number of days survival for a colony because trampling and predation were unlikely to operate independently between nests within a colony, and because anthropogenic disturbance and predator counts were conducted at the level of the colony. The best model was then checked using Mayfield logistic regression: total number of failed nests/total number of exposure days for each colony was then substituted as the dependent variable and a binomial logistic regression carried out.

Thirdly, we used GLMs to determine whether brood-stage chick survival was correlated with the mean of any habitat measurements collected per brood (dominant vegetation type, vegetation height, proportion of dung cover, proportion of bare ground cover and distance to nearest water; distance to nearest village was not measured for broods). The analysis included hatch date to control for seasonal effects, and each brood was considered to be an independent sampling unit as broods did not merge. Variables at $P \geq 0.15$ were then removed from the models and a minimum adequate model was obtained. The best model was then checked using Mayfield logistic regression: whether chick stage succeeded or failed/number of exposure days was then substituted as the dependent variable and a binomial logistic regression carried out.

Finally, we examined Sociable Lapwing nest and brood habitat selection relative to factors that affected concealment and therefore survival. We compared mean nest or brood habitat values (dominant vegetation type, vegetation height, proportion of dung cover and proportion of bare ground) with mean values sampled from random points at 500 m from the nest using either chi-squared tests or *t*-tests.

All data were analysed using SPSS (Norusis 1998) or SAS (SAS Institute 2000) and according to Sokal and Rohlf (1981). All probabilities quoted are two-tailed and R^2 values are adjusted. Data are presented in the form mean \pm 1 se.

RESULTS

Spacing between nests and between colonies

There were 3.7 ± 0.6 nests per colony (range 1–8, $n = 58$ nests, $n = 15$ colonies). The mean distance between nests was 154 ± 26 m ($n = 12$ colony means, excluding single isolated nests, 4.4 ± 0.6 nests per colony). The mean distance between colonies was 3.1 ± 1.1 km ($n = 16$ colonies, range 706–19 000 m); if a single outlier is ignored then mean distance between colonies was 2.1 ± 0.4 km ($n = 15$ colonies). Colonies were located on average 1.2 ± 0.3 km from villages and 0.8 ± 0.2 km from water.

Attendance at the nest

Both female and male birds were seen incubating but this was not quantified to minimize disturbance. The proportion of time spent incubating in a 24-h sample period was 0.77 ± 0.02 , with 1.6 ± 0.2 trips off the nest per hour ($n = 13$ nests sampled for 24 h). The mean length of incubation periods was 48 ± 13 min and the mean length of time the nest was unattended was 11 ± 2 min ($n = 19$ nests).

Daily survival rates of eggs and chicks

In total, 36 nests out of 58 failed, with a total exposure of 635 days: daily nest survival rates were therefore 0.943 ± 0.009 . The number of exposure days per nest (e.g. an index of survival) did not vary significantly between colonies ($F_{15,42} = 0.9$, $P = 0.55$). Of 11 nests where we had a reasonable idea of the cause of failure, 64% were apparently trampled by cattle, goats or horses, 9% were depredated by birds, 18% by mammals (not including one nest that probably failed because a village dog was following a fieldworker) and 9% were deserted (in this case the ringed female was seen later in the season). One nest failed at 03:00 h as recorded by a temperature probe, suggesting a nocturnal mammalian predator. In total 12 broods of 36 failed, with a total exposure of 830 days: daily brood survival rates were 0.986 ± 0.004 . The number of exposure days per brood did not vary significantly between colonies ($F_{13,24} = 1.3$, $P = 0.28$).

Clutch size, and duration of the incubation and brood periods

Clutch size was 3.7 ± 0.09 eggs ($n = 58$ nests); if

only the 11 nests found before clutch completion are considered (i.e. that will not have been subject to any egg loss before clutch size was measured) then clutch size was 3.8 ± 0.1 eggs.

The mass and size of the eggs in eight nests found before clutch completion were measured at varying stages in the incubation period to establish the relationship between mean egg density of a clutch and days from clutch completion: days from clutch completion = $[(-3.27 \times 10^{-6}) \times (\text{mean of egg } \{\text{mass}/[(\text{width} \times \text{width}) \times \text{length}]\}) + 0.00052]$, $F_{1,6} = 52.6$, $n = 8$ nests, $P < 0.001$, $R^2 = 0.88$. This relationship was then used to establish the date of clutch completion for nests found after clutch completion, and then, by adding the observed clutch size (assuming one egg laid per day), the duration of incubation: mean duration of incubation was 28.6 ± 0.3 days ($n = 58$ nests). If only the 11 nests found before clutch completion are considered then incubation duration was 28.0 ± 0.7 days.

The period from hatching to fledging was determined by examining the change in mass of broods with time: mass = $[148.7 + (12.7 - 148.7)/\{1 + \exp[(\text{days since hatch} - 14.5)/3.9]\}]$, $\chi^2 = 82.7$, $R^2 = 0.97$, $P < 0.001$, $n = 23$ means of different ages in days from hatching. The brood period was estimated from the number of days at which the asymptote of the relationship was reached as 29 days. The fledging period established from a subjective assessment of when each brood had become fully able to fly and behave as adults was 29.3 ± 0.3 days ($n = 26$ nests).

Number of breeding attempts per pair per year

The number of breeding attempts per year was estimated as the maximum possible, by assuming that any pair that failed before the last possible date on which a second clutch could be started did indeed attempt to breed again. Clutch completion dates are illustrated in Figure 1. The first clutch was completed on 25 April and the last on 11 June: there was no clear unimodal pattern of clutch initiation dates, suggesting that re-nesting could be occurring after nest failure. Assuming a minimum average re-nesting interval of 8 days (based on data for the Northern Lapwing, see Cramp & Simmons 1983) and a further 3 days to complete the clutch, then 17 nests failed before 1 June, the last possible date after which a failing pair could have started a new nest. Fifteen nests were initiated after this date, and if the re-nesting interval is decreased to 5 days (as occurs at

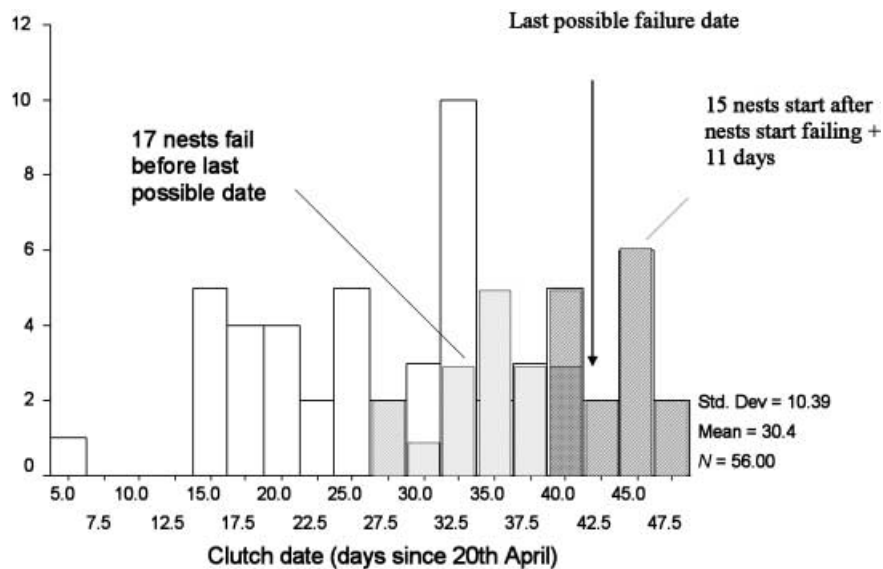


Figure 1. Histogram of clutch completion dates. The black arrow indicates the approximate last possible day that any failed pair prior to this could have started another nesting attempt before the last observed completed clutch (11 June minus 11 days to account for a re-nesting interval of 8 days plus a further 3 days to complete the clutch). The light hatched bars indicate the failure dates of the 17 nests that failed before the last possible re-nest opportunity. The dark hatched bars indicate those nests that were available that could have been re-nests: if an 8-day re-nesting interval is considered then only 15 nests were available that could have been re-nests, but if a 5-day re-nesting interval is considered then 18 nests were available.

the end of the breeding season for many waders) then 18 nests were initiated after this date, indicating that the estimated maximum re-nest frequency of 17 nests was possible. If 17 nests were 're-nests' then 34 of the 58 nests found were from 17 pairs. Therefore, the remaining 24 nests were from 24 pairs, making a total of 41 pairs responsible for 58 nests. There were thus a maximum of 1.41 breeding attempts (58/41) per pair.

Number of chicks produced per successful breeding attempt and per pair

On average, 3.0 ± 0.2 eggs hatched ($n = 22$ nests) from nests that survived to hatching and 2.2 ± 0.2 chicks ($n = 26$ broods) fledged from broods in which at least one chick survived for 29 days. If there were 1.41 breeding attempts per pair per year then each pair fledged on average 0.38 chicks per year.

Does observed productivity predict the decline in population?

In order to calculate the net population change from year to year we need to estimate productivity (number of new individuals gained per year) as we have done above, and also mortality (number of individuals lost

per year). We assumed that adult annual survival rates of Sociable Lapwing were a mean of those for Northern Lapwing (0.75) and Golden Plover (0.73): these estimates represent the only accurate survival estimates available for similar species (Sandercock 2003). We assumed that first-winter survival rates for Sociable Lapwing were the same as for Northern Lapwing (0.60): this represents the only accurate first-winter survival estimate available for a similar species (Peach *et al.* 1994). Both Northern Lapwing and Golden Plover are closely related species with very similar mass, latitudinal breeding location and migratory behaviour (see Cramp & Simmons 1983).

We then estimated that for every 100 adults (50 pairs), 25.9 are lost each year, and of the 19 chicks that 50 pairs would fledge every year, only 11.4 would survive their first year to breed. Therefore, in total the population should decline by 14.5% (11.4 gained minus 25.9 lost per 100 adults) per year. Therefore, if the survival rates we used are similar to those of the Sociable Lapwing and assuming the maximum possible re-nesting rate, then the decline in population observed is predicted well by the observed productivity (Fig. 2a). If the minimum rate of re-nesting (no re-nests) is used then the population decline is predicted to be steeper than observed (Fig. 2a). If adult survival is decreased by 0.1 then

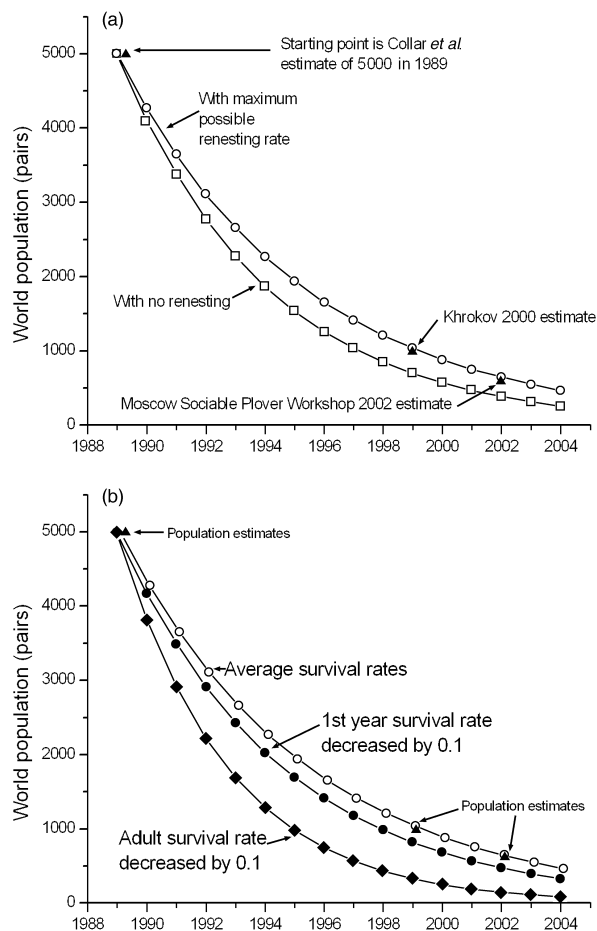


Figure 2. The observed decline in the number of pairs of Sociable Lapwing globally since 1989. Filled triangles represent the three observed population estimates. (a) The open circles represent the predicted decline in the population using observed productivity of 0.27 chicks per breeding attempt, the maximum possible re-nesting rate of 1.4 and an estimated survival rate of 0.74 adults and 0.6 first-years based on data from two similar mass shorebird species: all values remain constant over time. The open squares represent the predicted decline using the same values except with no re-nesting. (b) The filled circles represent the predicted decline in the population using an estimated survival rate of 0.64 adults and 0.6 first-years and the filled diamonds using an estimated survival rate of 0.74 adults and 0.5 first-years, all models using observed productivity of 0.27 chicks per breeding attempt and the maximum possible re-nesting rate of 1.4. The open circles show the same decline as in (a) above.

the population decline is predicted to be much steeper than observed, and decreasing first-winter survival by 0.1 also has a similar but less severe effect (Fig. 2b).

If the population is to remain stable, using the assumed survival rates above and maximum re-nesting rates, then Sociable Lapwings would have to

increase chick productivity by 2.3 times the current productivity to 0.87 chicks per pair. If we reverse the arguments within this model and ask what survival rate of adults is needed for the population to stay stable at the observed productivity then adult survival must be 0.89 per year assuming maximum re-nesting rates and 0.91 assuming no re-nesting.

Correlates of nest survival rate

The number of days that a nest survived until failure (or hatch) was significantly dependent on the dominant vegetation type around the nest, with nests surviving on average 5.6 days longer in *Artemisia* (controlling for colony and clutch completion date, Table 1); nests apparently also survived longer earlier in the season. A Mayfield logistic regression analysis to confirm the model in Table 1, however, did not identify either vegetation type ($\chi^2_1 = 1.9$, $P = 0.16$) or date ($\chi^2_1 = 0.2$, $P = 0.64$) as significant predictors of nest survival. The discrepancy in the results between the two model approaches is likely to have been a consequence of nest searching starting about 2 weeks after the first clutch was completed. The difference in results for vegetation type may then be because some high-survival nests found early in the season will have had few days over which nest survival could be determined simply because they were found well after clutch completion. This bias therefore operates to reduce the effect of vegetation in the Mayfield logistic regression model. The difference in the results for date of clutch completion may similarly be because early failing nests could not have been found early in the season. The bias therefore operates to increase the effect of date in the GLM.

The mean number of days that nests within a colony survived until failure (or hatch) was significantly dependent on the mean proportion of bare ground around the nests (positively: Fig. 3a), the number of potential nest predators (positively: Fig. 3b) and the number of cattle (negatively: Fig. 3c) (see Table 2). There was also a trend for the number of adult predators to correlate positively with colony survival (Table 2). A Mayfield logistic regression analysis to confirm the model in Table 2 broadly confirmed these results. The total Mayfield nest survival rate per colony increased significantly as the proportion of bare ground increased (parameter estimate = 0.06 ± 0.03 , Type III $\chi^2_1 = 5.3$, $P = 0.021$) and decreased significantly as the number of cattle increased (parameter estimate = -1.5 ± 0.6 , Type III $\chi^2_1 = 6.0$, $P = 0.014$); there was no significant effect of number of potential nest

Table 1. The effect of vegetation type around the nest (two-level factor, *Artemisia*- or grass-dominant), controlling for clutch completion date (season) and colony (as a random factor to control for nests being clumped) on the number of days that a nest survived.

Dependent variable: number of days survival from clutch completion						
Source		Type III sum of squares	df	F	Significance	Parameter estimates
Intercept	Hypothesis	2367.9	1	59.2	< 0.001	38.4
	Error	1438.4	36.0			
Colony	Hypothesis	913.2	15	1.6	0.14	
	Error	1204.0	31			
Vegetation type	Hypothesis	222.5	1	5.7	0.022	<i>Artemisia</i> 5.6
	Error	1204.0	31			
Clutch date	Hypothesis	427.5	1	11.0	0.0023	-0.4
	Error	1204.0	31			

Variables removed from the model were: mean vegetation height, $F_{1,26} = 2.1$, $P = 0.15$; mean proportion of dung cover, $F_{1,26} = 0.5$, $P = 0.49$; mean proportion of bare ground, $F_{1,26} = 0.5$, $P = 0.33$; distance to water, $F_{1,26} = 1.9$, $P = 0.18$; distance to village, $F_{1,26} = 1.8$, $P = 0.19$.

Table 2. The effect of mean proportion of bare ground around nests, the abundance of nest predators and the abundance of cattle at a colony on mean number of days that nests survived in a colony.

Dependent variable: mean number of days survival from clutch completion					
Source	Type III sum of squares	df	F	Significance	Parameter estimates
Corrected model	145.9	3	5.4	0.018	
Intercept	0.3	1	0.03	0.86	-1.27
Mean proportion bare ground	77.2	1	8.5	0.015	0.39
Cattle index	77.8	1	8.6	0.015	-7.27
Nest predator index	115.3	1	12.7	0.005	0.43
Error	90.7	10			
Total	5594.9	14			
Corrected total	236.6	13			
$R^2 = 0.50$					

Variables removed from the model were: mean availability of *Artemisia*, $F_{1,6} = 1.4$, $P = 0.28$; mean vegetation height, $F_{1,6} = 1.0$, $P = 0.37$; mean clutch completion date, $F_{1,6} = 0.5$, $P = 0.51$. The index of adult predators was significant in the full model, $F_{1,6} = 7.1$, $P = 0.038$ ($B = 5.3 \pm 2.0$), but not in the minimal model above, $F_{1,9} = 5.1$, $P = 0.051$.

predators (parameter estimate = 0.05 ± 0.4 , Type III $\chi^2_1 = 2.1$, $P = 0.14$), although the trend was for nest survival to increase as the number of nest predators increased.

The number of days that a brood survived until failure (or hatch) was significantly dependent on the dominant vegetation around the brood (higher survival where there was a higher proportion of *Artemisia*) and survival time decreased significantly later in the season (Table 3). A Mayfield logistic regression analysis to confirm the model in Table 3, however, did not find a significant effect of vegetation type on survival ($\chi^2_1 = 1.5$, $P = 0.23$) but did confirm the significant decline in chick survival later in the

season (parameter estimate = 0.07 ± 0.03 , Type III $\chi^2_1 = 5.6$, $P = 0.017$). The result that brood survival decreased later in the season may have arisen partly because later broods were recorded fledging earlier (the first 50% of nests to fledge successfully did so after 30.6 ± 1.2 days, compared with 28.5 ± 0.9 days for the last 50%; $t_{21} = 1.4$, $P = 0.17$).

Nest and chick habitat selection

The availability of habitat did not differ significantly at 10 m from that at 500 m from each nest, although there was a trend for vegetation to be taller at 500 m from the nest (Table 3). Nests were sited significantly

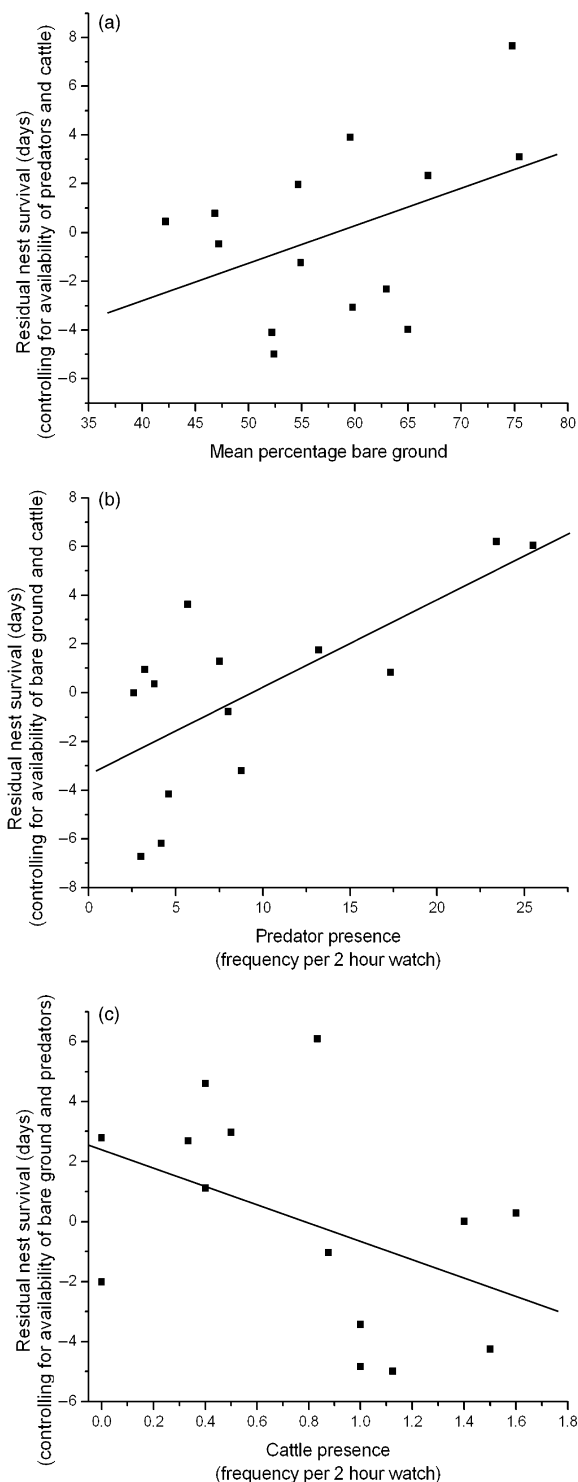


Figure 3. Significant predictors of nest survival at the colony level. (a) The mean proportion of bare ground, (b) the abundance of nest predators (corvids or gulls) and (c) the abundance of cattle. Each graph illustrates an effect shown in Table 2 and plots the residuals of a regression controlling for the other two significant predictors of nest survival.

more often in areas dominated by *Artemisia* rather than grass and in areas with a significantly higher percentage of dung cover, but nests were randomly sited with respect to percentage 'cover' of bare ground (Table 4). There was a trend for nests to be sited in shorter vegetation (Table 4). Chicks were more likely to be located in areas with a significantly lower percentage of bare ground, but were located randomly with respect to *Artemisia* or grass, or percentage dung cover (Table 4). The bare ground result is not an artefact of there being more bare ground available later in the season when the chick location records were collected, compared with the random point measurements that were conducted mainly during the earlier nest stage (GLM of percentage bare ground with season as covariate, $F_{1,52} = 0.9$, $P = 0.36$). There was a trend for chicks to be located in areas with taller vegetation (Table 4). This result is not an artefact of vegetation being higher later in the season when the chick location records were collected, compared with the random points measurements that were conducted mainly during the earlier nest stage, because vegetation height decreased significantly with season ($y = -11x + 10.4$, $F_{1,52} = 11.6$, $R^2 = 0.17$, $P < 0.001$).

DISCUSSION

This study has quantified a number of aspects of the breeding biology of the Sociable Lapwing for the first time, although much of what we found is very similar to previous more anecdotal studies, suggesting that our study may be fairly typical for breeding over the last few decades. We quantified nest survival rates of the Sociable Lapwing for the first time and found that survival rates during the egg stage are particularly low, and appear to be sufficient to account for the decline in the population. Low nest survival rates appear to be due to the Sociable Lapwing's preference for nesting in highly grazed habitats, where grazer density remains high during nesting, with a concomitant high risk of nest disturbance and trampling. Formerly, such areas were probably created across a wide area of Kazakhstan without the grazers remaining in the area during nesting because of nomadic herding. Nowadays grazing is non-nomadic, and Sociable Lapwing nesting habitat is restricted to near settlements where grazer density remains very high throughout the breeding season. Physical protection of nests or temporary reduction in grazer density in colonies during the egg stage is the logical first step to halt the population decline.

Table 3. The effect of mean dominant vegetation type (two-level factor $\geq 50\%$ and $< 50\%$ *Artemisia*) controlling for hatch date (season) on the number of days that a brood survived. Note that sample size of broods ($n = 32$) here is less than the total number of broods because vegetation selection data were not collected for four broods.

Dependent variable: number of days survival from hatch date					
Source	Type III sum of squares	df	F	Significance	Parameter estimates
Corrected model	769.5	2	6.3	0.005	
Intercept	2892.8	1	47.7	< 0.001	28.1
Vegetation type	279.3	1	4.6	0.040	<i>Artemisia</i> 6.2
Hatch date	581.0	1	9.6	0.004	-0.38
Error	1759.0	29			
Total	22034.4	32			
Corrected total	2528.6	31			
$R^2 = 0.26$					

Variables removed from the model were: mean vegetation height, $F_{1,25} = 0.01$, $P = 0.93$; mean proportion of dung cover, $F_{1,25} = 0.04$, $P = 0.84$; mean proportion bare ground, $F_{1,25} = 1.6$, $P = 0.21$; distance to water, $F_{1,25} = 0.8$, $P = 0.38$.

Table 4. Habitat measurements at the nest and for broods compared with random points. *P*-values in bold type are those that are significant after a sequential Bonferroni correction, $K = 3$ tests each of four hypotheses (see Rice 1989).

Value or frequency for:	Dominant vegetation		Vegetation height	Percentage dung	Percentage bare ground
	<i>Artemisia</i>	Grass			
Random points at 10 m	28	30	6.0 ± 0.3	1.5 ± 0.3	60.1 ± 2.4
Random points at 500 m	21	37	8.8 ± 1.3	2.2 ± 0.4	54.4 ± 3.0
10 m vs. 500 m χ^2 or <i>t</i> -value	1.7		-2.2	-1.5	1.5
10 m vs. 500 m <i>P</i> -value	0.19		0.03	0.12	0.13
Nest	32	19	6.0 ± 0.4	9.5 ± 1.1	56.5 ± 3.0
Nest vs. 500 m χ^2 or <i>t</i> -value	7.7		-2.3	6.0	0.7
Nest vs. 500 m <i>P</i> -value	0.006		0.02	< 0.001	0.5
Brood	17	28	13.3 ± 1.1	1.9 ± 0.4	43.5 ± 2.5
Brood vs. 500 m χ^2 or <i>t</i> -value	0.03		2.5	-0.8	-2.8
Brood vs. 500 m <i>P</i> -value	0.87		0.03	0.44	0.007

Breeding biology of the Sociable Lapwing

Many parameters recorded in this study are consistent with the previous but largely qualitative or limited studies of the Sociable Lapwing. Colony size in our study (3.7) is similar to that of 4 from Khrokov (1977), but less than the 4–5 pairs described for the 1970s to 1980s by Gordienko (1991). Khrokov (1996) estimated inter-nest distances in one colony as 80–300 m, and our mean inter-nest distance was 154 m. Nests in our study were located 1.2 km from villages compared with 200 m on average (Khrokov 1977) and 2–4 km for 80% of nests (Gordienko 1991); nests described in Khrokov (1996) were between 1 and 1.5 km from water compared with our mean of 0.8 km.

Although attendance is described as biparental in Cramp and Simmons (1983), and there are indeed many observations of males incubating (including this study), it now seems clear that incubation is mainly uniparental, with the male only contributing a very small proportion of incubation (Gordienko 1991, Khrokov 1996). Khrokov (1996) recorded a 75.1% ($n = 988$ min) attendance rate for a single female, which is similar to our rate of 77.0%, but recorded an average trip duration of 27 min compared with our mean duration of 11 min.

First and main laying dates in our study are similar to previous records, 20 April to 1 May (Khrokov 1996) and 29 April to 25 May (Gordienko 1991), with fresh clutches being recorded throughout June (Ryabov 1949). Re-nesting rates in another

study were possibly at least 1.2 attempts per pair (Gordienko 1991), although this estimate is very approximate; our maximum rate was 1.4. Clutch size in our study was 3.7 compared with 3.4 eggs for Khrokov (1996) and 3.9 ($n = 27$) for Gordienko (1991). Clutch size in the 1930s was 4.17 ($n = 66$) with 12 nests having five eggs (Ryabov 1949); plover clutches of five are recorded, although unusually (Cramp & Simmons 1983), and may also reflect 'egg-dumping', a situation perhaps to be expected in a colonial species. Reported incubation periods lie between 21 days (Zarudny 1888, reported in Khrokov 1977) and 25 days (Kozlova 1961), but none has been estimated properly prior to this study: our period from complete clutch to hatch was, however, similar, estimated at about 24.6 days.

Gordienko (1991) found that 44% of nests with eggs ($n = 26$) failed: our equivalent rate is 61% failure of nests found with eggs before hatch ($n = 56$); the difference in frequencies between the two studies is not significant ($\chi^2_1 = 2.4$, $P = 0.12$).

Gordienko (1991) and many other anecdotal reports described nesting habitat preference as very similar to that identified in this study: 96% of nests ($n = 130$) were located in 'Artemisia, and Salicornia with an admixture of fescue grass *Festuca sulcata*', in 80–90% bare ground and predominantly low vegetation of < 10 cm height, although Gordienko (1991) reported this as less than 25 cm height.

Overall, it seems reasonable to conclude that the characteristics of Sociable Lapwing breeding have not changed over the last few decades, with the possible exception of clutch size, which may have decreased by 11% since the 1930s. This decrease, if true, may be a consequence of current reduced colony size reducing the opportunity for alternative breeding strategies such as 'egg-dumping', rather than a change in mean productivity per pair. Therefore, our study may well represent a Sociable Lapwing breeding situation similar to any studied over the period of the species' decline.

Causes of the population decline

Sociable Lapwings have very low probability of nest survival during the egg stage, but have similar probability of chick survival as other shorebird species that do not have rapidly declining populations (Berg 1992, Peach *et al.* 1994). The survival rates of eggs and chicks in this study are sufficient to account

for the population decline. This analysis is based on a number of assumptions, the most uncertain, and the one unfortunately of greatest effect, being adult survival rate (see Fig. 2). However, an adult survival of 0.89 would be required at current productivity for the species population to break even each year. Although such adult survival rates are possible, for example 0.9 in Black-tailed Godwit *Limosa limosa* (see Sandercock 2003), they are not typical for a much smaller shorebird species. It seems much more likely that adult Sociable Lapwings in a declining population have relatively low survival rates, yet if they are lower than average and if rates of productivity estimated in this study are representative (and sample sizes are large of both nests and colonies), then the rate of population decline is likely to be greater than currently estimated. Clearly, estimates of adult and first-winter survival rates of Sociable Lapwing are needed, and our colour-ringing of adults and chicks may allow these to be calculated in future years. At the present time, however, we can only assume average survival rates.

Positive correlates of nest survival included the mean proportion of bare ground and possibly also the presence of *Artemisia* as dominant vegetation. Nesting Sociable Lapwings also positively selected areas where *Artemisia* was dominant, and areas where there was a higher proportion of dung. These results suggest that heavily grazed ground is the preferred nesting habitat: heavy grazing is likely to promote *Artemisia* dominance over grass (because it is relatively unpalatable) and to increase bare ground, and the amount of dung is a very good correlate of grazer density (Laing *et al.* 2003, Young *et al.* 2005). Negative correlates of nest survival include the number of grazers present during the egg stage. Earlier studies have also reported nests in heavily grazed areas, as well as nest failures due to cattle disturbance (Gordienko 1991, Khrokov 1996), and have suggested the importance of this mechanism in the population decline (Shevchenko 1998). This presents a contradiction: Sociable Lapwings actively select heavily grazed areas and its vegetation characteristics promote nest survival, yet the presence of grazers results in decreased nest survival. This apparent paradox may be explained by Sociable Lapwings having evolved to exploit habitats created by nomadic or migratory herbivores: they require heavily grazed vegetation to establish the habitat for nesting, but not the continued presence of grazers. Where grazers are nomadic or migratory, a situation of heavily grazed areas followed by the absence of grazers will be common. This is

likely to have been the evolutionary and historical situation, first as a response to the niche created by large herds of migratory Saiga Antelope *Saiga tatarica* (at least in the southern parts of the Sociable Lapwings' range), and latterly by the nomadic horse- and cattle-grazers present in Kazakhstan until recently (Robinson & Milner-Gulland 2003). The time period for the rapid change from widespread nomadic herders to settled collective farms and indeed the substantial decline of the Saiga Antelope population from the 1930s onwards (Robinson & Milner-Gulland 2003) coincide well with the period of decline of the Sociable Lapwing: during the 1930s the species was still extremely common in Kazakhstan but has declined substantially since then (Ryabov 1949, 1974). This process may have been facilitated by an increasing aridity in the region, making marginal nesting habitat unsuitable and forcing Sociable Lapwing and domestic livestock into the same areas (Shevchenko 1998). Sociable Lapwings appear to have evolved for a highly specialized niche that involves nesting on ground prepared by intensive grazing, and as a result now nest in areas close to villages, where grazers remain throughout the nesting period and in many places are herded out to pasture and back across colonies every day, resulting in extremely high trampling risk.

A further positive correlate of nest survival is the abundance of avian nest predators (and also probably avian adult predators). Nest predators have been implicated in the failure of Sociable Lapwing nests anecdotally (Gordienko 1991, Khrokov 1996), and indeed contributed to some nest failures in our study, but none of the previous Sociable Lapwing studies has attempted to relate variation in predator numbers to nest survival. Nest predation on shorebirds is the norm for many species (e.g. Byrkjedal 1987, Larsen 1991, Berg 1996) and may not be associated particularly with declining populations (Parr 1993). Our results strongly suggest that nest predators (and probably adult predators) are not a major cause of low breeding success in Sociable Lapwing, as nests with higher numbers of predators in the area actually survive for longer (or at the very least were not affected by predator numbers). Instead, it seems likely that nest predators such as gulls and crows (and also probably raptors such as harriers) are attracted to areas with high numbers of cattle for the same reason as the Sociable Lapwings, and indeed the cattle themselves: these areas probably represent good habitats for all of these species because of higher productivity there.

Conservation management

Further years of nest survival data need to be collected to confirm the results of this study and the effects of any change in the number of grazers. Colour-ringing of the population to establish survival rates is also an absolute priority. But if our data are representative, and assumptions of survival rates accurate, then the case is compelling that it is trampling and nest disturbance by high grazer numbers that is mainly responsible for the decline in the Sociable Lapwing population. The next logical step in arresting the decline of the species is therefore management of grazer numbers when nesting colonies are established in late April and early May. Grazers should be excluded from colonies where possible from about the last week in April until the last week in June: we would predict that hatching success will be greatly improved and overall breeding success will then be sufficient to result in a population increase for the managed birds. Ideally, this would be done in an experimental way, with some colonies left as controls to confirm the effect of grazer pressure on nesting success, but considering the critically endangered nature of the Sociable Lapwing, it is perhaps better to reduce grazer density to all possible populations immediately.

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