Research paper

Surviving in sprawling suburbs: Suburban environments represent high quality breeding habitat for a widespread shorebird

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HIGHLIGHTS

- Compared breeding ecology of native shorebird in agricultural and suburban environments.
- Suburban birds were more likely to make distraction and aggression displays.
- Suburban females were in better condition and reproductively successful than agricultural ones.
- A few species may benefit from urban sprawl though they are likely to be exceptions.

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ABSTRACT

Throughout the world, urban sprawl converts agricultural land to urban environments, however, little is known of the influence of such landscape change on the reproductive success of native species. We predicted that reproductive success would be suppressed by urban sprawl through habitat degradation and indirectly through compromised quality of parental care from human disturbance. We studied the masked lapwing, *Vanellus miles*, a common ground-nesting species that occurs in both agricultural and suburban landscapes. Contrary to our predictions, parents in suburban environments invested more in defence of eggs (aggression and distraction) yet suburban female lapwings were in better condition (7% heavier) and laid 2% longer eggs than agricultural female lapwings, suggesting greater access to food resources in suburban than agricultural environments. Lapwings had higher hatching success in suburban compared with agricultural environments, leading to greater reproductive success; a similar rate of chick mortality was evident between environments. The conversion of land from agriculture to suburbia results in species which are winners and losers, some of which (e.g., for species such as the ground-nesting lapwing) are difficult to predict *a priori*. Despite an overall trend of decreasing avian diversity with increasing urbanisation world-wide, suburban environments have the capacity to act as high quality breeding habitat for species such as the masked lapwing, although such species may be the exception rather than the rule.

1. Introduction

Urbanisation is considered one of the leading causes of species extinction (Czech, Krausman, & Devers, 2000). However, the concept of urbanisation encapsulates a broad range of land-use changes, from the conversion of native vegetation to densely populated cities, to the transformation of agricultural environments to low density, suburban environments; the latter process being known as 'urban sprawl'. Although urban sprawl is widespread, particularly in developed countries, its impact on native species has received sparse attention in the literature (Blair, 2004).

One reason for this might be that agricultural environments are perceived as containing little in the way of biodiversity (Fischer, Lindenmayer, & Manning, 2005). However, in many parts of the world, such environments are critical habitats for native species. For example, 'countryside elements' (*sensu* Daily, 1997), such as agricultural plots, gardens, fallow land, and plantations, can act as habitat for a range of native species; for instance mammals in Central America (Daily, Ceballos, Pacheco, Suzan, & Sanchez-Azofeifa, 2003; Daily, Ehrlich, & Sánchez-Azofeifa, 2001), and birds in Europe (Fuller, Bennett, & Ramsden, 2004; Fuller, Trevelyan, & Hudson, 1997) and Australia (Haslem & Bennett, 2008).

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Not only can urban sprawl result in local extinction due to changes in landscape structure, it also introduces many novel disturbances which can disrupt reproduction and survival rates of those species that are able to persist within urbanised environments; for example depredation by domestic pets, such as cats (Churcher & Lawton, 1987), and disturbance from humans and their vehicles (Baumann, 2006; Purcell & Verner, 1998; Ruhlen, Abbott, Stenzel, & Page, 2003). Parental care is one life history trait affecting the demography of many bird species, as it represents a significant cost during reproduction and strongly influences the survival of offspring (Clutton-Brock, 1991). Disruption to parental care can lead to reduced fitness and lower reproductive success (Price, 2008; Safina & Burger, 1983).

Here, we study the influence of urban sprawl on a native species of common shorebird; the masked lapwing, *Vanellus miles*. This species is an interesting case-study in faunal response to urban sprawl for several reasons. First, it is one of a limited number of native bird species that are able to persist in both agricultural and suburban environments. Second, it exhibits high levels of biparental care, and thus, disruptions to breeding may have direct fitness consequences (Chambers, Gibbs, Weston, & Ehmke, 2008; Marchant & Higgins, 1993). Finally, it nests on the ground, and therefore is potentially susceptible to processes characteristic of human-dominated environments, such as depredation by domestic pets and disturbance by human visitation (Baumann, 2006; Purcell & Verner, 1998; Ruhlen et al., 2003).

We hypothesised that although the masked lapwing is able to persist within suburban environments, it might do so at a cost. Specifically, we made two predictions regarding the influence of urban sprawl on parental investment and reproductive success on the basis of the species' life-history, which we test with empirical data derived from monitoring of the species' reproduction and parental care in both agricultural and suburban environments. Firstly, we predicted that adults in suburban environments would invest more into parental care than those in agricultural environments due to higher rates of novel processes (e.g. human visitation, depredation by pets) that evoke active defence of eggs and young. Increased parental investment will result in suburban adults having poorer condition and lower quality of parental care (e.g. incubation constancy) than those in agricultural environments, unless sufficiently abundant resources offset such effects. Secondly, this reduced condition of adults, and the lower quality of parental care, is likely to reduce the reproductive output of individuals in suburban environments. In avian species this is expressed as a reduction in the probability of eggs hatching and of chicks fledging (Carney & Sydeman, 1999). Other processes more common to suburban than agricultural environments, such as actual depredation of eggs and chicks by domestic pets, are likely to compound this effect further.

2. Materials and methods

2.1. Study area

This study was undertaken on Phillip Island, southern Victoria, Australia (38°28′32″ S, 145°12′12″ E), during the 2010 winter breeding season of the masked lapwing, which runs from May to September (Chambers et al., 2008). Phillip Island has an abundant population of masked lapwings inhabiting agricultural and suburban environments. Suburban and agricultural environments are quite distinct because peri-urban environments are uncommon on the island. Suburban environments are characterised by relatively high-density housing and roads, whereas agricultural environments are characterised by open farmland and few houses. Suburban environments on Phillip Island consist of a number of small settlements found within an agricultural environment. A representative population density for a suburban settlement on Phillip

Island is 280 people per km^2, while Phillip Island has an overall population density of 71 people per km^2; the majority of whom occur within small settlements.

2.2. Locating breeding pairs, nests and broods

Breeding pairs were located by systematic searching from vehicles and by foot. Upon nest or brood discovery (nests, 71; brood only, 33), GPS co-ordinates were recorded along with the number of eggs/chicks. Eggs were numbered with a non-toxic fine felt-tipped permanent marker (Szekely, Kosztolanyi, & Kupper, 2007) and four measurements were recorded: mass (±0.1 g; spring balance), length and maximum width (±0.01 mm; dial callipers) and float angle (float chamber; to estimate egg age; Hoyt, 1979; Liebezeit et al., 2007). Nests were assigned to one of two habitat types: (1) 'suburban', any environment with built-up human dwellings within 50 m of the nest, often bound by fences; or (2) 'agricultural', any environment outside of suburban boundaries and more than 50 m from human dwellings, with territories often including farmland and with few or no human dwellings.

2.3. Environmental variables

In addition to habitat type (i.e. agricultural or suburban), we measured a number of environmental variables at each nest deemed likely to influence parental care and reproductive success. Nest characteristics measured included: the maximum height of grass (±1.0 mm) directly next to the nest (Willson et al., 2001); distance to roads (Rheindt, 2003), recorded in metres using a laser rangefinder; and maximum air temperature experienced during the course of each 24 h period of incubation (Cantar & Montgomerie, 1985). Temperature was measured using Ibutton^{TM} temperature loggers and nearby weather stations. To record ambient temperature, a temperature logger was placed *ca.* 20 m distant from the nest in a shaded, sheltered, position 30 cm above the substrate. Temperature loggers took readings every 30 min, and remained at the nest until eggs had hatched or failed. A maximum temperature for each day (24 h) was then extracted from the data recorded by the ambient temperature loggers. Temperature loggers were placed at a subsample of 21 nests (suburban, 11; agricultural, 10) that were also being video monitored (see details on video monitoring below). At sites without temperature loggers, maximum temperatures were obtained from weather stations on Phillip Island at the Penguin Parade (~0.6–2.0 km from sites) and in Rhyll (~1.0 km from sites) (Bureau of Meteorology, 2010).

2.4. Capture, marking and sexing

Adults were captured at nests once laying had ceased using a walk-in wire funnel trap placed over the nests (an adaptation to the cage trap described by D'Andria, 1965). This technique allowed the trapping of one parent per nest, with 45 out of 46 attempts being successful. The average time for an adult to enter the trap and incubate the nest was approximately 35 min. No eggs were abandoned as a result of trapping. Adults were marked with unique bicoloured leg flags (engraved with an alpha–alpha sequence) on the tibia and a standard metal band on the tarsus. Blood samples of up to 50 μl were taken from the tarsal vein for molecular sexing. Individuals were genetically sexed using the CDH1 gene recommended for non-ratite birds (Supplementary file 1; Fridolfsson & Ellegren, 1999).

2.5. Estimating adult condition

A set of measurements of adults were recorded upon capture: tarsus plus toe (±0.5 mm) and mass (±1 g). The residuals of a

Generalised Linear Model (GLM) between adult mass and tarsus plus toe were then used as an index of adult condition; we follow the approach of Schulte-Hostedde, Zinner, Millar, and Hickling (2005) who use such indices of body condition to assess the mass of an individual, indicative of energy reserves, relative to its structural size.

2.6. Prediction 1: the quality of parental care is higher in agricultural than suburban environments

2.6.1. Incubation and brood attendance

We consider incubation and brood attendance as measures of parental care because they significantly affect offspring survival and incur a cost to parents (Clutton-Brock, 1991). A subsample of nests (21 nests; suburban, 11, agricultural, 10) were randomly selected to be monitored by video to determine incubation behaviours. Temperature loggers were placed at all nests that were video monitored (17 loggers were retrieved; suburban, 9, agricultural, 8). An infrared video camera was placed *ca.* 2 m away from the nest on a short stake (25 cm high), and it recorded continuously for 3 days. The amount of time that parents spent either incubating or away from the nest was recorded. Days with 'initial absences' (i.e. those caused by the investigator) longer than 100 min were outliers and were excluded from the analysis. Where the duration of video footage fell below 1000 min in any one day (due to equipment difficulties), the entire day was excluded from the data set. Thus, 8 days were excluded and 55 days of observation were used in the analysis.

Brood attendance (n = 43 broods; suburban, 25, agricultural, 18) was determined by the proximity of adults to the brood (i.e. broods were 'attended' if adults were ≤5 m from their chicks). Each known brood was observed from a vehicle every 10 days (10.01 ± 0.56 days between observations; from 1 to 30 days old). The occurrence of brood attendance was recorded, when possible, for a total of 79 observations (suburban, 49; agricultural, 30).

2.6.2. Parental defence

We consider parental defence as a measure of parental care because it affects offspring survival and represents a cost to parents (Clutton-Brock, 1991). A measure of parental defence was made each time an investigator approached a breeding pair. The presence or absence of aggressive behaviour (defined as swooping within 5 m of the investigator) and distraction displays were recorded (see Marchant & Higgins, 1993 for a description of behaviours) during 235 visits (suburban, 132; agricultural, 103) to 71 nesting pairs and during 88 visits (suburban, 57; agricultural, 31) to 54 brood-rearing pairs. A visit was an observation of parental defence behaviour when adults were disturbed by an investigator approaching a nest or chicks. There were less 'visits' to agricultural breeding pairs because they were easier to monitor from a distance without an investigator needing to approach the nest and chicks. The brood-rearing pairs observed included breeding pairs that were discovered during the incubation stage, whose chicks had since hatched, and those that were only discovered during the brood-rearing phase. Any observation where chicks were older than 40 days was excluded from the analysis because of low sample sizes after this age. Chicks were aged on the basis of known hatching dates or growth curves (after Glover, Weston, Maguire, Miller, & Christie, 2011).

2.7. Prediction 2: reproductive success is higher in agricultural than suburban environments

2.7.1. Hatching success

We assessed hatching success using infrared motion sensor cameras (5MP ultra compact digital scouting cameras) and repeat-surveys. All nests that were video monitored (n = 21 nests) received an infrared camera when video equipment was removed. An additional 12 randomly selected nests received infrared cameras, so that 33 nests (suburban, 16; agricultural, 17) were monitored with infrared cameras in total. All other nests were monitored by repeat-surveys. Cameras allowed long-term unobtrusive monitoring of nests, allowing the cause of nest failure to be determined. Nests with cameras were checked for incubating birds every three to five days to confirm whether eggs had hatched or failed, and to inform the timing of camera removal. The nest was inspected if chicks were observed, or if incubating birds were consistently absent from the nest over a three-day period. Images were used to determine egg fate and hatching date. Where cameras were not used, nests were checked from a distance every one to two days until chicks were seen or eggs were confirmed missing. The number of eggs that hatched at each nest was determined from the number of chicks observed in or near the nest, the number of remaining eggs, or the fate of each egg as determined from video recordings.

For nests where hatching date was known, egg age at discovery was estimated from an analysis of float stage and days to hatching (r^2 = 0.85, t = −12.53, $P \leq 0.001$, days to hatching = −2.87 × float stage + 33.11). Egg volume was estimated from values of egg length and width following Hoyt (1979).

2.7.2. Fledging success

Forty-one nests had a known brood size at hatching. A total of 158 chicks were measured from known nests and pairs discovered during brood-rearing; any chick over seven days old was excluded from the analysis due to uneven sampling above this age. Thus, 69% (n = 109 chicks; suburban, 68; agricultural, 41) of chicks were used to analyse differences in chick condition and 56% (n = 89 chicks; suburban, 62; agricultural, 27) of chicks were used to analyse fledging success between habitat types. Upon capture, chicks were marked with a metal band, and a measure of tarsus (±0.01 mm) and mass (±1 g) were taken, along with a blood sample. As with adults, the residuals of a GLM between chick mass and tarsus were used as an index of chick condition (following Johnsen, Delhey, Andersson, & Kempenaers, 2003). Chicks were released at the capture location and were only captured once. Where hatching date of chicks was unknown, chicks were aged using available growth rates (Dann, 1981; Glover et al., 2011).

Fledging success was determined using repeated surveys of each brood. Each brood that was monitored for fledging success was observed once a week (6.97 ± 0.53 days between observations; during the first 30 days after hatching) and the number of chicks present was recorded. If a brood could not be seen, a search of the area was made until the brood (and marked parents, where applicable) was located or was determined to have died. On repeated observation of broods with unmarked parents, broods were considered to be the same if chicks possessed metal bands. This is consistent with the observation that broods stay within a territory maintained by the parents and that chicks from different broods were never found mixed together. Chicks were considered to have died if parents of a young brood were observed without chicks on at least three consecutive occasions, this was only determined for breeding pairs where parents could be identified by a bicoloured leg flag. Chicks were considered to have fledged if they were seen flying or were at an age when they were capable of flight (six weeks of age). Chick fate was recorded as unknown if chicks were not seen to fledge and parents and chicks were not seen after 2–3 searches of their location.

2.8. Statistical analysis

Each nest or brood was regarded as independent during analyses. In some instances, several measures were taken from

Table 1
A list of predictor variables that were used in the analyses conducted by this study with the response variable(s) that they were modelled with. The references provide justification as to why the predictor variable was included in the model with the corresponding response variable.

Predictor variable/Covariate (CV)	Response variable	Reference
Tarsus plus toe length	Adult mass	Ebbinge and Spaans (1995)
Sex (male/female)	Adult mass	Owens and Hartley (1998)
Days to hatching (eggs/nests)	Egg mass	Hoyt and Rahn (1980)
	Time absent from nest	Moreno (1989)
	Occurrence of aggression	Cilento and Jones (1999) and Knight et al. (1987)
	Occurrence of distraction	Cilento and Jones (1999) and Knight et al. (1987)
	Egg hatching success	Young (1963)
Maximum temperature	Time absent from nest	Cantar and Montgomerie (1985)
Distance to road	Time absent from nest	Reijnen, Foppen, and Meeuwsen (1996), Rheindt (2003) and van der Zande, ter Keurs, and van der Weijden (1980)
Maximum grass height	Time absent from nest	Willson et al. (2001)
Presence of camera	Egg hatching success	Richardson, Gardali, and Jenkins (2009)
Age of chicks	Chick mass	Dann (1981)
	Occurrence of two adults attending brood	Székely and Cuthill (1999)
	Occurrence of aggression	Cilento and Jones (1999) and Knight et al. (1987)
	Occurrence of distraction	Cilento and Jones (1999) and Knight et al. (1987)
	Fledging success	Hunt and Hunt (1976) and Young (1963)
Brood size	Occurrence of two adults attending brood	Nur (1984); Wiklund (1990)

a single location (e.g. hatching of multiple eggs within a nest), resulting in non-independence of data. To account for this, we used Generalised Linear Mixed Models (GLMMs), specifying location (i.e. nest or brood) as a random effect, and predictor variables as fixed effects (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). General Linear Models (GLMs) were used where data points were independent (e.g. nests). Response variables in regression models were binary indicators of hatching success (e.g. 0 = did not hatch, 1 = hatched), fledging success, survival and parental defence, which were specified as having a binomial distribution of errors and a logit link function. Response variables were modelled as a function of habitat type, which was included as a categorical variable with two levels (i.e. suburban and agricultural), in addition to other predictor variables as appropriate (Table 1). Model fit was estimated from marginal ($R^2_{GLMM(m)}$) and conditional ($R^2_{GLMM(c)}$) coefficients of determination, following Nakagawa and Schielzeth (2013). $R^2_{GLMM(m)}$ estimates model fit using fixed effects only, while $R^2_{GLMM(c)}$ estimates model fit including both fixed and random effects. Egg age and egg mass are correlated because egg mass decreases with age; as such, when determining an effect of habitat type on egg mass, we included age as a covariate. Similarly, chick age and chick mass are correlated because chick mass increases with age; as such, when determining an effect of habitat type on chick condition (model residuals of chick mass and tarsus plus toe length) we included chick age as a covariate.

Where appropriate, data were tested for normality and homogeneity of variances. Regression models were generated using the statistical software package R 2.11.1 and 2.15.0 (R Development Core Team, 2010). GLMMs were generated using glmmPQL, within the package MASS (Venables & Ripley, 2002). See Supplementary Table 1 for a list of all the models tested and Supplementary Table 2 for comprehensive information on sample units and size for each model.

3. Results

A total of 104 distinct breeding pairs were located (nests, 71 and brood only, 33). Only one repeated nesting attempt was included in analysis. No brood was seen using both habitat types (n = 54, includes broods hatching from monitored nests, and those discovered as broods). Nests were distributed across the island; suburban nests were found within four distinct human settlements, with a maximum distance of ~13 km between suburban nests, and a maximum distance of ~14 km between agricultural nests. The minimum distance between suburban and agricultural nests was ~200 m. We

captured 45 adults and genetically determined the sex of 39 individuals (7 suburban males and 14 suburban females; 12 agricultural males and 6 agricultural females); results were inconclusive for six individuals due to poor DNA quality.

3.1. Prediction 1: the quality of parental care is higher in agricultural than suburban environments

3.1.1. Parental condition

There was a significant interaction between habitat type and sex on condition (GLM; interaction, df = 35, P = 0.027). However, contrary to our prediction that adult condition would be lower in suburban environments, female condition was significantly higher in suburban compared with agricultural habitat types (suburban, 398.36 ± 6.30 g; agricultural, 371.33 ± 9.63 g) while, for males, condition did not differ between habitat types (suburban, 401.86 ± 8.91 g; agricultural, 410.50 ± 6.81 g).

3.1.2. Incubation and brood attendance

A subsample of 21 (from 71) nests were monitored for a total 1369 h. The amount of time lapwings were absent from the nest did not vary significantly with habitat type, days to hatching, the distance to the nearest road, or maximum grass height around the nest (Table 2). There was a significant relationship between time spent off the nest and the maximum temperature during an observation session, with nests being attended less when the maximum temperature was higher (Table 2). The presence of adults attending a brood was recorded on 79 occasions from 43 brood-rearing pairs. This measure was not recorded for all brood-rearing pairs. There was no significant difference in parental brood attendance between habitat types, the number of chicks present, or the age of chicks (Table 2).

3.1.3. Parental defence

Suburban birds were more likely to engage in both aggression and distraction compared with agricultural birds (Table 2). The number of days until hatching had no effect on the occurrence of either aggression or distraction (Table 2). Neither habitat type nor chick age influenced the occurrence of parental aggression during brood-rearing; however, parents were more likely to make a distraction response when they tended younger chicks (Table 2).

Given that suburban female birds are in better condition and have greater parental defence during incubation and brood attendance, we reject our first prediction that the quality of parental care is higher in agricultural environments than in suburban environments.

Table 2
Results from Generalised Linear Mixed Models investigating the influence of habitat type and additional selected predictor variables on two response variables which correspond to the stage-specific reproductive success of masked lapwings. Model fit was estimated from marginal ($R^2_{GLMM(m)}$) and conditional ($R^2_{GLMM(c)}$) coefficients of determination, following Nakagawa and Schielzeth (2013). $R^2_{GLMM(m)}$ estimates model fit using fixed effects only, while $R^2_{GLMM(c)}$ estimates model fit including both fixed and random effects. For all models the agricultural environment, in habitat type, is set as the reference variable. df = degrees of freedom; C = coefficient; SE = standard error; T = test statistic; no. samples = the number of samples and unit used in the model, with the number of breeding pairs in brackets (see Supplementary Table 1 for greater detail of sampling). Emboldened values represent significant results.

Response variable	Predictor variable	df	C	SE	T	P	No. samples
Egg hatching success	Habitat	53	2.73	1.11	2.45	**0.017**	210 eggs
($R^2_{GLMM(m)} = 0.13$; $R^2_{GLMM(c)} = 0.80$)	Days to hatching	53	−0.12	0.06	−1.99	0.052	(58)
	Camera presence	53	2.14	1.26	1.70	0.095	
Fledging success	Habitat	24	−0.99	1.14	−0.87	0.395	89 chicks
($R^2_{GLMM(m)} = 0.09$; $R^2_{GLMM(c)} = 0.66$)	Age of chicks	24	0.37	0.25	1.48	0.152	(27)
Overall survival	Habitat	40	2.89	1.35	2.13	**0.039**	141 fledglings
($R^2_{GLMM(m)} = 0.17$; $R^2_{GLMM(c)} = 0.78$)	Days to hatching	40	−0.01	0.08	−1.44	0.158	(45)
	Camera presence	40	1.99	1.56	1.27	0.210	
Time absent from nest	Habitat	18	−2.10	27.12	−0.08	0.939	55 days
($R^2_{GLMM(m)} = 0.16$; $R^2_{GLMM(c)} = 0.62$)	Days to hatching	31	−2.63	2.28	−1.15	0.258	(21)
	Maximum temperature	31	7.17	2.90	2.48	**0.019**	
	Distance to road	31	0.38	0.65	0.59	0.562	
	Maximum grass height	18	−0.07	0.14	−0.53	0.603	
Occurrence of two adults attending brood	Habitat	41	0.49	0.61	0.80	0.427	79 observations
($R^2_{GLMM(m)} = 0.03$; $R^2_{GLMM(c)} = 0.25$)	Age of chicks	34	−0.02	0.02	−1.08	0.286	(43)
	Brood size	34	<−0.01	0.25	−0.01	0.991	
Occurrence of aggression during incubation	Habitat	162	2.65	0.67	3.94	**<0.001**	235 visits
($R^2_{GLMM(m)} = 0.15$; $R^2_{GLMM(c)} = 0.71$)	Days to hatching	162	−0.01	0.02	−0.59	0.554	(71)
Occurrence of aggression during brood-rearing	Habitat	52	0.55	0.51	1.06	0.292	88 visits
($R^2_{GLMM(m)} = 0.03$; $R^2_{GLMM(c)} = 0.03$)	Age of chicks	33	−0.04	0.02	−1.57	0.125	(54)
Occurrence of distraction during incubation	Habitat	162	2.62	0.65	4.05	**<0.001**	235 visits
($R^2_{GLMM(m)} = 0.20$; $R^2_{GLMM(c)} = 0.63$)	Days to hatching	162	0.03	0.02	1.41	0.161	(71)
Occurrence of distraction during brood-rearing	Habitat	52	0.96	0.86	1.11	0.272	88 visits
($R^2_{GLMM(m)} = 0.12$, $R^2_{GLMM(c)} = 0.65$)	Age of chicks	33	−0.10	0.04	−2.73	**0.010**	(54)

Significant P values below 0.05 are in bold.

3.2. Prediction 2: reproductive success is higher in agricultural than suburban environments

We detected no significant difference in clutch size (suburban, 3.66 ± 0.07 eggs; agricultural, 3.63 ± 0.07 eggs; GLM, $t_{67} = 0.79$, $P = 0.435$), egg width (suburban, 35.78 ± 0.06 mm; agricultural, 35.86 ± 0.09 mm; GLMM, $C = −0.05$, SE = 0.17, $t_{66} = −0.29$, $P = 0.777$, $R^2_{GLMM(m)} \leq 0.01$, $R^2_{GLMM(c)} = 0.67$) or egg volume (suburban, 32.94 ± 0.12 mm^2; agricultural, 32.45 ± 0.13 mm^2; GLMM, $C = −0.72$, SE = 0.41, $t_{66} = 1.15$, $P = 0.254$, $R^2_{GLMM(m)} = 0.01$, $R^2_{GLMM(c)} = 0.64$) between habitat types. However, eggs from suburban environments were longer compared with eggs from agricultural environments (suburban, 50.36 ± 0.19 mm; agricultural 49.49 ± 0.15 mm; GLMM, $C = 0.88$, SE = 0.35, $t_{66} = 2.49$, $P = 0.015$, $R^2_{GLMM(m)} = 0.05$, $R^2_{GLMM(c)} = 0.47$). Egg length and width were not strongly correlated ($r = 0.05$, $P = 0.420$). There was no difference in egg mass between habitat types when egg age (a key driver of egg mass) was included in the model as a covariate (suburban, 31.44 ± 0.22 g; agricultural, 30.15 ± 0.32 g; GLMM, $C \leq 0.01$, SE = 0.07, $t_{170} = 0.07$, $P = 0.942$, $R^2_{GLMM(m)} = 0.16$, $R^2_{GLMM(c)} = 0.83$).

3.2.1. Hatching success

Of the 71 nests discovered, 61 (suburban, 30 nests; agricultural and 31 nests) were identified as having succeeded (i.e. one or more eggs hatched) or failed (i.e. 0 eggs hatched), while the fate of ten nests could not be ascertained. Of 222 individual eggs that were followed through the experimental period, 133 hatched (suburban, 76; agricultural, 57). Twelve eggs (3 nests) were excluded from analysis due to unnatural human interference or because there was insufficient evidence to confidently assign fate. Therefore, 210 eggs (suburban, 105; agricultural, 105) from 58 nests (suburban, 29; agricultural, 29) were included in the analysis of hatching success. Habitat type significantly influenced the probability of an egg hatching (Table 2), with eggs being more likely to hatch in suburban

environments compared with agricultural environments (Fig. 1). There was a marginally non-significant trend for the probability of hatching to be influenced by the age of a clutch at first discovery (i.e. 'days to hatching', Table 2).

Of the 89 failed eggs, egg fate was determined for 77 eggs from 31 nests (suburban, 11; agricultural, 20). Five fate types were identified: "abandonment", "human interference" (hatching failure caused by human activity), "depredation", "crushed by stock", and "unknown" (Table 3). The unknown category refers to eggs that did not hatch and for which the cause of failure was unknown.
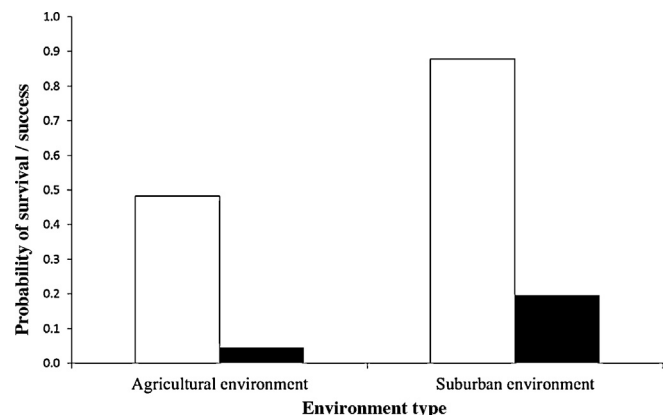

Fig. 1. Results from Generalised Linear Mixed Modelling of the probability of: (1) a masked lapwing egg hatching (open bars), and (2) a masked lapwing egg surviving to fledging (black bars) in agricultural and suburban environments. The probability of an egg hatching was predicted from success and failure of 210 eggs (suburban, 105; agricultural, 105) from 58 nests (suburban, 29; agricultural, 29). The probability of an egg surviving to fledging was predicted from the success and failure of 45 breeding-pairs (suburban, 22; agricultural, 23). There was no significant difference in clutch size (suburban, 3.66 ± 0.07 eggs; agricultural, 3.63 ± 0.07 eggs; GLM, $t_{67} = 0.79$, $P = 0.435$) or fledging success (GLMM, $t_{24} = 24$, $P = 0.395$) between environments.

Table 3
All of the egg fates recorded and the number of nest and egg failures that were caused by each fate type by habitat type. The percentage (%) of fate shows how much each habitat type contributed to each fate type, e.g. 50% of abandonment occurred in suburban and agricultural environments, whereas, 100% of depredation occurred in agricultural environments.

Fate	Suburban environment			Agricultural environment		
	No. Nests	No. eggs	% of fate	No. Nests	No. eggs	% of fate
Abandonment	10	22	50	10	22	50
Human interference	1	4	100	–	–	–
Depredation	–	–	–	3	10	100
Crushed by stock	–	–	–	4	10	100
Unknown	1	6	67	3	3	33

3.2.2. Fledging success

Fledging success was determined for 127 chicks (39 broods). Chicks older than seven days at first discovery were excluded from the analysis because of a significant difference in the age of chicks at discovery between habitat types ($t_{125} = -0.808$, $P = 0.044$), and the age of chicks at discovery significantly influenced the probability of fledging, whereby older chicks were substantially more likely to survive to fledging (GLMM including all samples; $C = 0.13$, $SE = 0.05$, $t_{36} = 2.76$, $P = 0.009$). Thus, 70% (89 chicks from 27 broods; suburban, 18 broods; agricultural, 9 broods) of the total number of chicks recorded to fledge were used to compare fledging success between habitats. The probability of fledging did not differ between habitat types (Table 2). Similarly, there was no significant difference in brood size between habitat types ($t_{39} = -0.06$, $P = 0.114$), with breeding pairs in suburban environments containing 3.26 ± 0.23 chicks, as compared with 3.28 ± 0.18 in agricultural environments. There was no significant difference in chick condition between habitat types when age was included in the model (GLMM, $C = -0.09$, $SE = 0.20$, $t_{70} = -0.47$, $P = 0.639$, $R^2_{\text{GLMM(m)}} = 0.02$, $R^2_{\text{GLMM(c)}} = 0.73$).

3.2.3. Reproductive success

In total, 141 eggs (suburban, 65; agricultural, 76) from 45 breeding pairs (suburban, 22; agricultural, 23) were followed from egg to fledging or failure. There was a significant difference in overall survival between habitat types (Table 2), with the probability of an egg producing a fledgling being greater in suburban environments than agricultural environments (Fig. 1). Overall survival refers to the survival of an egg from discovery in a nest to fledging or failure. Given that overall survival was greater in suburban environments, we reject our second prediction that reproductive success will be higher in agricultural environments compared with suburban environments.

4. Discussion

Despite an overall trend of decreasing avian diversity with increasing urbanisation world-wide (Chace & Walsh, 2006), suburban environments have the capacity to act as high quality breeding habitats for some native species (this study). Even with presumed increased costs associated with higher levels of parental care in suburban than agricultural areas, suburban female lapwings were in better condition and laid larger eggs than their agricultural counterparts. These two factors are likely to have contributed to another unexpected finding; that eggs in suburban environments have a higher probability of hatching than eggs in agricultural areas, contributing to higher overall reproductive success in suburban than agricultural environments.

The increased probability of eggs hatching in suburban environments is likely to have resulted from two inter-related processes: (1) greater female condition in suburban environments, leading to higher quality eggs being laid, as evidenced by larger eggs in suburban than agricultural environments; and (2) differing amounts of, and effectiveness of, nest defence between habitats.

Although avian species richness is reduced during urban sprawl (Marzluff, 2001), a small number of species often become locally abundant (Blair, 1996; McKinney, 2008). One possible mechanism explaining such a trend is an alteration in key food resources. Steinberg, Pouyat, Parmelee, and Groffman (1997) showed that earthworms, a key component of lapwing diet (Marchant & Higgins, 1993), occurred at higher densities within urban than agricultural environments. An increase in food resources (i.e. earthworms) is consistent with suburban female lapwings having greater body condition and producing larger eggs; suggesting food resources may play a crucial role in overall reproductive success (Barker & Vestjens, 1990; Blomqvist, Olof, & Götmark, 1997). It is possible that suburban female masked lapwings have greater access to food resources than their agricultural counterparts, allowing them to invest more in breeding. One caveat is that if resource availability alone was contributing to higher female condition, suburban males should experience a similar benefit; however, this was not observed. We are unsure as to why this disparity exists, but may be related to uneven sampling of sexes between habitat types. Alternatively, the energetic investment of females in breeding may be greater than for males (i.e. through the production of eggs) and so poorer condition in relation to limited food resources may only be exhibited among females.

The better body condition of suburban female lapwings can result in greater hatching success in two ways. Firstly, individuals in better condition can invest greater resources into the production of eggs, resulting in higher quality eggs being laid which may lead to a greater chance of hatching (Parsons, 1970). Secondly, greater female condition may buffer such birds from the larger investment they make in parental care, allowing greater quality care (Whittingham & Dunn, 2000). Indeed, parental care may be a more important factor in reproductive success than egg size (see Christians, 2002). The fact that both female condition *and* parental defence were higher in suburban environments suggests that female masked lapwings in suburban environments have access to resources over and above their agricultural counterparts. That is, female lapwings in suburban areas must have substantially greater access to food resources if they are in better condition despite having to allocate more energy to parental defence. Although sample sizes regarding female condition are relatively small, the effects are striking, and we suggest future research investigate this further.

Urban sprawl affects parental care by changing the threats associated with breeding. In particular, ground-nesting birds are vulnerable to the threats of urban sprawl because nests and young are exposed and easily accessible to predators, potentially increasing the cost of care. Costs associated with care will influence the effort that parents contribute to defence (Montgomerie & Weatherhead, 1988). If defence is more costly or less effective in agricultural environments because adult condition is lower, or because predators or intruders are perceived as more dangerous and incur more risk (i.e. cost) to the parent, this would lead to lowered parental defence. Masked lapwings in suburban environments may have learned to selectively target humans perceived

as 'threatening', such as those walking towards the nest, but do not respond (i.e. have habituated or adapted; Weston, McLeod, Blumstein, & Guay, 2012) to humans that are not perceived as threatening, such as those walking along a footpath (Glover et al., 2011; Warne & Jones, 2003). Therefore, contact with humans may not be considered a threat per se (Müllner, Eduard Linsenmair, & Wikelski, 2004). This behaviour is similar to the Australian magpie *Gymnorhina tibicen* and American crow *Corvus brachyrhyncho* which show greater rates of defence against humans where human disturbance is greatest (Cilento & Jones, 1999; Knight, Grout, & Temple, 1987). Among suburban birds, an increase in nest defence may at least partly explain increased egg success in suburban environments.

Urban sprawl causes a change in predator communities, whereby large birds (e.g. corvids) represent a high proportion of nest predators in suburban environments (Ryder, Reitsma, Evans, & Marra, 2010) and mammals associated with human habitation, such as dogs, cats and rats, would presumably be at higher densities. Lapwing eggs may avoid depredation by large birds because the parents themselves are large and therefore able to defend effectively against predators of comparable size (Green, Hirons, & Kirby, 1990). Human-associated mammals may not prey upon lapwing eggs because adults are able to effectively defend nests. Parental defence was not effective against livestock where stock crushing was a major cause of egg mortality (Cardilini and Weston, unpublished data), and livestock disturbance may provide predators with more opportunities to take eggs (Hart, Milsom, Baxter, Kelly, & Parkin, 2002). High levels of stock disturbance co-occurred with high levels of depredation in this study. One notable feature of Phillip Island is the extremely low density of foxes (*Vulpes vulpes*), which prey upon the eggs and young of ground-nesting bird species (Angelstam, 1986; Kirkwood, Dann, & Belvedere, 2000). If foxes were present in higher densities on the island, suburban birds may have had lower reproductive success because fox densities in urban habitats are high (Brunner, Lloyd, & Coman, 1975; Brunner, Moro, Wallis, Andrasek, & Andrasek, 1991). A comparison with mainland Australia, much of which has high fox densities, would reveal any influence foxes might have on suburban reproductive success.

Studies that consider the influence of urbanisation on fledging success often deal with altricial birds (in which chicks are fed by parents) (Rottenborn, 2000; Tella, Hiraldo, Donazar-Sancho, & Negro, 1996; Wilcove, 1985) rather than precocial species (in which chicks are capable of feeding themselves), for which measuring chick fate is extremely difficult due to high chick mobility (Gregg, Dunbar, & Crawford, 2007; Ruhlen et al., 2003). We found no difference in fledging success between habitats despite other studies showing precocial chicks experience greater mortality with higher rates of human disturbance (Baumann, 2006; Ruhlen et al., 2003). For precocial species, parental defence decreases soon after hatching possibly because it is difficult to defend scattered young or because chicks become less vulnerable as they age (Andersson, Wiklund, & Rundgren, 1980; Dowling & Weston, 1999; Gramza, 1967; Stephen, 1963). With a decrease in parental defence, chicks in suburban environments may be just as susceptible to depredation as rural chicks, thus, balancing survival rates between habitats during this stage. This is consistent with our finding that parental aggression differed between suburban and rural lapwings only during incubation, but was similar in both areas during brood-rearing. Despite similar chick survival, overall reproductive success of masked lapwings was higher in suburbs, in part due to the greater hatching success of suburban lapwings. This greater hatching success means that, although similar numbers of chicks are lost during brood-rearing, suburban environments will produce a greater number of chicks which fledge per adult, than agricultural environments.

Species that benefit from urbanisation are the exception rather than the rule, and the negative impacts of habitat modification and urbanisation on native species far outweigh its benefits (Chace & Walsh, 2006). The positive relationship that masked lapwings experience with suburban environments on Phillip Island occurs at relatively low housing densities, compared with housing densities found in large cities, and we caution that any increase in housing density may alter this relationship. The predictions we made at the outset of this study require further testing on a variety of species; their lack of application described here cannot be generalised. From a management and planning perspective, understanding the mechanisms behind lowered reproductive success is as important as identifying the reduction in reproduction. Knowledge of which mechanisms reduce reproductive success would permit a targeted plan for reducing the effect of such processes on reproduction. For instance, if success is being severely influenced by compromised life history traits, such as parental care, disturbances during these periods of reproduction may be managed within a human dominated setting to mitigate negative effects on reproductive output (e.g. through the establishment of temporary buffers, see Dowling & Weston, 1999). We suggest that future research target a variety of species exhibiting different responses to urban sprawl, with a view to examining the life history characteristics that predispose species to expansion, existence or extinction in the suburban matrix.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2013.04.001.

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