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Quantifying density dependence in a bird population using human disturbance

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Abstract Although density dependence has long been recognised as vital to population regulation, there have been relatively few studies demonstrating it spatially in wildlife populations, often due to the confounding effects of variation in habitat quality. We report on a study of woodlarks *Lullula arborea*, a species of European conservation concern, breeding on lowland heath in Dorset, England. We take the novel approach of utilising the birds' response to human disturbance, which resulted in much of the variation in density but had no direct impact on demographic rates. Within years, in sites with greater density there were smaller mean chick masses, lower post-fledging survival, and higher rates of nestling mortality attributed to starvation. The effects on clutch size and fledging success were confounded by the area of grassland within a site. There was no effect on brood size. Density dependence also operated within sites between years: as density increased there were reductions in mean chick mass and post-fledging survival, while nestling mortality attributed to starvation increased. Density-dependent effects on clutch size were only weakly regulatory, whereas density-dependent starvation and post-fledging mortality rates contributed strongly to differences in overall breeding output. Heavier chicks (when 7 days old) were significantly more likely to fledge and less likely to starve. Broods with heavier chicks were more likely to supply recruits to the breeding population. Nestling mass was not a factor in survival in the immediate post-fledging period, suggesting that density-dependent processes act independently on this stage. We conclude that the number of birds per hectare of suitable habitat is a valid means of expressing density, and that habitat acts as a surrogate for food abundance through which density dependence operates on the woodlark population.

Keywords Clutch size · Chick weight · Post-fledging survival · Starvation · Recruitment

Introduction

It has long been realised that density-dependent processes play a vital role in the regulation of wildlife populations (Lack 1954). Furthermore, understanding the effects of density dependence is vital if one is to predict the population consequences of a change in conditions, such as habitat loss or increased human disturbance (Sutherland and Norris 2002).

Although of fundamental importance, density dependence is difficult to detect in natural populations (Newton 1998). There are four main approaches, all of which have associated difficulties:

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1. Relating change in population growth rate to population size cannot distinguish density dependence from the response expected from census error unless census error has been measured, which in practice is very difficult.
2. Relating between-year changes in components of birth and death rates to temporal changes in density is the best approach. For example, many studies have shown clutch size decreases at high density for a wide variety of avian taxa (e.g. Stenning et al. 1988; Cooch et al. 1989; Both et al. 1999; Kruger and Lindstrom 2001). This approach requires a long and detailed data set, and can also be confounded if there are other changes in the habitat. Furthermore, measures of mean density in any 1 year underestimate additional density dependence arising through spatial variation.
3. Experiments are an excellent means of studying density dependence. However, they can be expensive, can raise ethical issues and are most practical for certain groups, for example manipulating nest box densities in studies of tits *Parus* spp. and flycatchers *Ficedula* spp. (e.g. Alatalo and Lundberg 1984; Török and Tóth 1988; Both 1998a, b).
4. Measuring spatial variation in density and demography has the serious problem that it is likely to be confounded by a response of density to variation in habitat quality (e.g. Lindström et al. 2005). As higher densities are expected on better-quality sites the strength of density dependence may be underestimated, so that this method usually cannot be used to give sensible results (but see, for example, Stokes and Boersma 2000; Forero et al. 2002).

In the present study, we take a novel and alternative approach and utilise the spatial variation in density resulting from birds' responses to recreational disturbance. Mallord et al. (2007a) showed that the density of woodlarks *Lullula arborea* on heathlands in Dorset, southern England was reduced on sites with high levels of human disturbance, as a result of birds not nesting in the most heavily visited areas, although they continued to forage in such areas. In contrast, there was no direct effect of disturbance on breeding success or nest survival (Mallord et al. 2007a). Thus, once expressed in terms of the available suitable habitat, density is poorly related to site quality, and the resultant variation in density acts as a kind of natural experiment.

In territorial species, density dependence can be driven by two non-mutually exclusive processes: competition for resources and interference from neighbouring individuals (Lack 1947). In both cases, density dependence operates through inducing food shortages (e.g. Arcese and Smith 1988), and affects all stages of breeding, offspring health and recruitment (Both et al. 1999, 2000; Tella et al. 2001). However, relating abundance to the availability of such resources, or surrogates such as habitat area, is a common problem in detecting density (Newton 1998; Lindström et al. 2005). In the present study, we considered woodlark numbers in relation to the area of suitable habitat, as calculated by a model of woodlark habitat use (Mallord et al. 2007a). The model of habitat use relates foraging observations to vegetation structure and does not include any measures of disturbance. Although density is lower on disturbed sites due to avoidance of nesting in areas with high visitor use, woodlarks forage widely in areas of suitable habitat throughout such sites.

Here we report on a study of spatial density dependence, examined at each stage of the breeding process, for a population of woodlarks *L. arborea* breeding on lowland heath in Dorset, southern England. The woodlark has an unfavourable conservation status in Europe, which holds the majority of its global population (Birdlife International 2004). The Dorset population largely inhabits highly fragmented patches of heathland (Wotton and Gillings 2000), all that remains of a once far more extensive habitat (Webb and Haskins 1980; Rose et al. 2000).

Materials and methods

Study sites

On our study sites, woodlarks used forestry clearfells, recently burnt heathland patches, mown heather, short grassy fields, horse paddocks and areas of regenerating heathland that retain a substantial extent of bare ground (Mallord et al. 2007a).

A total of 16 heathland sites were used in this study. Due to the outbreak of foot and mouth disease during spring 2001, fieldwork did not start until mid-way through that season, so that only six sites were used in that year. Subsequently, an additional six sites were used in 2002 (total, $n = 12$), and a further four in 2003 (total, $n = 16$). Of these sites, three never supported breeding woodlarks in any year, and therefore were omitted from the analyses.

Woodlarks

The main focus of fieldwork was the location of nests, the finding of which automatically denotes the presence of a territory (Bibby et al. 2000; Gilbert et al. 1998). When a pair was present on a territory, a nest was subsequently found in all cases. Pairs were located at settlement and followed at regular intervals (at least weekly) throughout the pre-breeding period, when they spent some time off-site, but otherwise fed conspicuously as a pair. This gave us confidence that we found each pair's first nesting attempt in 2002 and 2003. Although very few territory holders were colour-ringed (2003, $n = 16$), we felt confident in assigning successive nests to individual territories, as pairs fed in the same areas throughout the entire breeding season. Based on the small sample of colour-ringed adults that were found holding territories in successive years (2003–2004, $n = 8$), there were no instances of between-year adult dispersal. Frequency of nest visits depended on the stage at which the nest was found. If the nest was located during the building or laying stages, it was checked every 4 days until it was close to hatching (14-day incubation period; Cramp 1980), when it was checked daily to obtain the exact date of hatching. If found during incubation, so that the laydate was not known, nests were checked every 2 days. The frequency of nest visits did not affect daily rates of nest survival (Mallord et al. 2007b). ''Laydate'' refers to the date of laying of the first egg and was recorded as the number of days from 1 March. It was usually determined by subtracting the 14-day incubation period [+ $(n - 1)$ days, where n = clutch size, to take account of the pre-incubation laying period] from the hatching date. In 17% of cases ($n = 36$), nests were found with a complete clutch and were then lost to predators prior to hatching: 1st egg date was then estimated from the mid-point of the range of possible lay dates (known from the number of days the clutch had been monitored). Clutch size was taken as the number of eggs in a finished clutch, i.e. after the female had started incubating. Brood size was measured as the number of hatched chicks. Chicks were noted as having died of starvation if they were found dead in or just outside of the nest before the time of fledging.

Woodlark density was measured as the number of pairs per hectare of suitable habitat. The area of suitable habitat on each site was calculated from a logistic model of woodlark habitat use (Mallord et al. 2007a). The majority of habitat utilised by woodlarks on all sites consisted of heathland vegetation ($\bar{x} \pm \mathrm{SD}; 70.3 \pm 26.9\%, n = 13$ sites), regenerating after a period of management (e.g. burning, mowing), with smaller proportions of forestry clearfell (17.9 ± 22.2%, $n = 13$) and short grassland, e.g. horse paddocks (11.4 ± 9.2%, $n = 13$). Habitat type was not retained in models of habitat suitability, which included measures of vegetation structure (Mallord et al. 2007a).

Chicks were ringed with a unique combination of colour rings in addition to a uniquely numbered metal ring and weighed (with a Pesola spring balance to the nearest 0.1 g) when they were 7 days old, i.e. when their legs were long enough to take the rings, but the birds were not so old that they would prematurely abandon the nest. Chick weight was taken as the mean weight of all chicks within each brood. Nest monitoring continued until the chicks fledged (usually at 11 days old), starved or were removed by predators. Fledging success was measured as the mean number of chicks fledged per pair per season for each site.

After fledging, we observed that juveniles spent up to 4 weeks accompanying their parents, sometimes until a second brood had hatched. Post-fledging searches for colour-ringed juveniles were carried out twice: firstly, at 10–14 days, and secondly, at 14–20 days. Adults would occasionally fly with the juveniles off the site during this period; therefore, the analysis only included those post-fledging searches in which adults were seen. Post-fledging survival was measured as the proportion of fledged chicks that subsequently survived the immediate post-fledging period. A total of 30 juveniles from 20 broods were recruited into the population between 2002 and 2004. None of these recruits came from broods that were thought not to have survived. Fourteen (70%) of these broods were seen during post-fledging searches, while in the other six (30%) cases the adults were not located during the immediate post-fledging period.

Recruitment was measured as the number of recruits into the subsequent year's breeding population per fledged chick for each natal site. Nestlings were individually colour-ringed during 2001–2003, and recruited 2002–2004. Although nests were not located during 2004, all study sites ($n = 16$) plus an additional 23 sites were searched for recruits during the breeding season of that year.

Only 16 birds out of a study population of 49 pairs (in 2003) were colour-ringed, so it was not possible to accurately quantify the age structure of the population. However, known first-year birds ($n = 13$) did not preferentially settle on sites with the highest density of birds (comparison between the seven sites with the lowest density and the six sites with the highest density, $\chi^2_1 = 0.7$, $P > 0.25$, with Yates' correction for 1 *df*). In addition, pairs comprising at least one known first-year bird did not have a lower reproductive success than all other pairs (clutch size, Mann–Whitney $U = 478.5$, $n = 90$, $P = 0.76$; fledged, $U = 134$, $n = 49$, $P = 0.39$). In fact, the number of nestlings starving per nest tended to be lower for known 1st year birds ($U = 240.5$, $n = 75$, $P = 0.06$). Therefore, although the sample size of colour-ringed birds is small, and the category ''other pairs'' may also include first-year birds from sites not monitored in this study, these results do suggest that effects attributed to density were not due to poorer performance of young birds.

Analysis

Following Aebischer (1999), probability of nest survival was modelled using a generalised linear model, with the nest's fate (failed or successful) as the dependent variable, binomial error terms and the number of days over which the nest was monitored as the number of binomial trials. The change in deviance in the model was treated as a χ^2-value to assess the significance of any density effect. As density was measured per site, observations were nested within sites to avoid pseudoreplication.

Non-parametric correlations were carried out between the proportion of the three main habitat types (i.e. heathland, clearfell and grassland) comprising a site's suitable habitat and the various measures of productivity and survival (Table 1). These showed that, although the proportions of heath and clearfell showed no relationship with breeding parameters, clutch size and mean chick mass may be influenced by the availability of grassland. Therefore, the proportion of grassland was controlled for in partial correlations of density with the measures of productivity and survival. The proportion of grassland was negatively correlated with density (Spearman's $R_s = -0.62$, $P = 0.025$, $n = 13$ sites). Each site could not be treated as independent between years, therefore mean values were used for each site ($\bar{x}$ density over 2 years, $n = 9$ sites, 2003 only, $n = 4$ sites). To control for seasonal variation in clutch size, analysis of density was performed using residuals from the quadratic regression of clutch size against laydate ($y = 2.9357 + 0.0346x - 0.0003x^2$; $F_{1,176} = 15.79$, $R^2 = 0.15$, $P < 0.001$), where x = the number of days since 1 March.

Table 1 Spearman's rank correlations between the proportion of suitable habitat made up of the various main habitat types for each study site and five measures of breeding productivity, for woodlarks breeding on 13 heathland sites in Dorset. Statistically significant *P*-value in *bold*

Breeding parameter	Proportion of suitable habitat		
	Heath	Clearfell	Grass
Clutch size			
R	–0.36	0.09	0.71
P	0.25	0.78	**0.01**
n	12	12	12
Mean chick mass			
R	–0.21	0.01	0.54
P	0.49	0.97	0.06
n	13	13	13
Proportion starved			
R	0.44	–0.34	–0.47
P	0.13	0.26	0.10
n	13	13	13
Post-fledging survival			
R	–0.32	0.30	0.46
P	0.35	0.36	0.15
n	11	11	11
Fledged			
R	–0.44	0.38	0.42
P	0.13	0.20	0.15
n	13	13	13

Results

Woodlarks laid two to five eggs, with the majority (64.5%) laying four; the mean clutch size was 3.87 (±0.47 SD, $n = 188$, data from all 3 years). Although there was a decline in residual clutch size as density increased (least squares regression, weighted by number of nests per site, $F_{1,10} = 9.9$, $r^2 = 0.5$, $P = 0.01$; Fig. 1a), the relationship disappeared when controlling for the proportion of grassland in a partial correlation ($r = -0.31$, $n = 13$, $P = 0.39$).

Unsurprisingly, brood size was correlated with clutch size (Spearman's $R_s = 0.62$, $n = 13$, $P = 0.04$). Although brood size was related to density, there was no separate effect of density once clutch size was controlled for in a partial correlation ($r = -0.38$, $n = 13$, $P = 0.25$).

There was much variation in the mass of chicks at 7 days old, ranging from 6.5 to 25.2 g (mean ± SD mass of chicks per brood, $\bar{x} = 15.7$ g $\pm$ 3.5, $n = 116$ broods). The mean mass of chicks per brood was lower at high densities (partial correlation controlling for grassland, $r = -0.81$, $n = 13$, $P = 0.002$; Fig. 1b). The effect of density on chick mass was not confounded by the effect of brood size (brood size vs. chick mass, Spearman's $R_s = 0.46$, $n = 13$, $P = 0.12$). There was also no effect of date on chick mass (chick weight vs. laydate, $F_{1,114} = 0.85$, $r^2 = 0.001$, $P = 0.78$).

Complete or partial starvation occurred in 51 out of 162 broods (31.5%). Of 204 nests found 109 failed, of which 67 (53.4%) were lost at the brood stage. Starvation accounted for 14 of these 67 failures (20.9%), the remainder failed due to predation. A total of 104 chicks were lost to starvation (out of 552 that hatched, 18.8%), 51 from complete loss of broods, and a further 53 chicks from 37 broods that suffered partial starvation. A total of 116 broods survived to 7 days old when they were weighed; of these, 29 (25%) contained chicks that subsequently starved, including the loss of ten complete broods. The mass of chicks that subsequently fledged was significantly greater than of those that later starved (mean ± SE, fledged, $\bar{x} = 16.8$ g $\pm$ 0.18, starved, $\bar{x} = 11.2$ g $\pm$ 0.38; $t_{313} = 13.6$, $P < 0.001$). Not surprisingly, the proportion of chicks that starved on each site, including chicks that died prior to being weighed at 7 days old, declined as the mean weight of chicks per brood increased (least squares regression, weighted by the number of chicks hatched; $F_{1,11} = 47.54$, $r^2 = 0.81$, $P < 0.001$; Fig. 1c). The loss of chicks to starvation also increased with density (partial correlation, $R_9 = 0.71$, $P = 0.015$; Fig. 1d). There was no effect of density on the

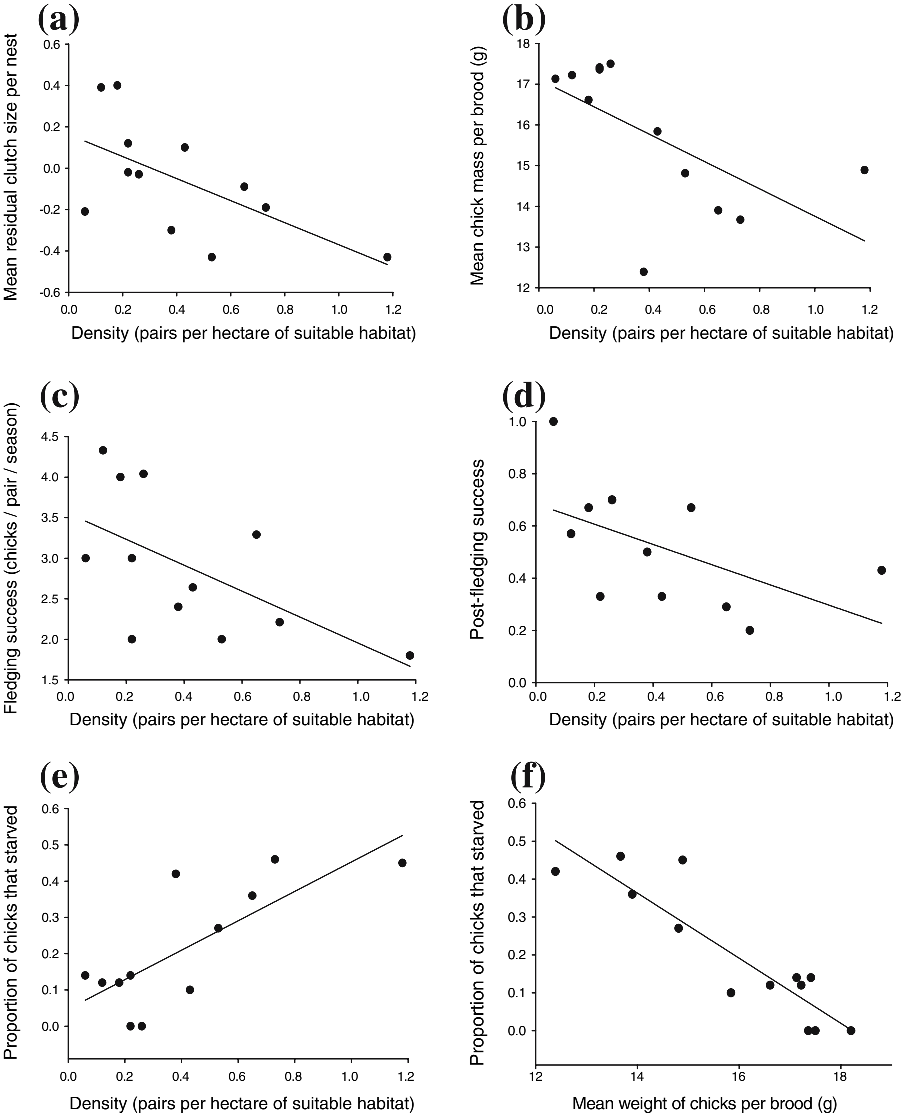

Fig. 1 The relationship between density of breeding woodlarks and **a** clutch size (residual variance from a quadratic model of clutch size against date of nest initiation); **b** the mean weight of chicks per brood (grams); **c** fledging success (chicks per pair per season); **d** the proportion of fledged juveniles seen during post-fledging searches; and **e** the proportion of nestlings that starved. **f** This shows the relationship between the mean weight of chicks and the proportion of nestlings that starved. Points represent mean values for each site for 2001-2003, except **c** and **d** for which data from 2002 and 2003 only were used

probability of a nest being predated ($\chi^2_2 = 0.55$, $df = 2$, $P > 0.75$, $n = 204$ nests).

A total of 29 pairs were present on nine study sites in 2002, and 44 pairs on 13 sites in 2003. The mean number of chicks fledged per pair (‘‘fledging success’’) was 3.28 (±2.52 SD) in 2002 and 2.93 (±2.07) in 2003. There was much variation between sites, mean fledging success ranging from 0 to 6.33 chicks per pair per site. Although there is a trend for fledging success to decline with increasing density (Fig. 1e), the relationship disappears when the proportion of grassland on a site is controlled for in a partial correlation ($r = 0.16$, $n = 13$, $P = 0.65$).

There was also a trend for the proportion of fledged chicks that were subsequently seen during post-fledging searches to decline (partial correlation, $r = 0.76$, $n = 13$, $P = 0.018$; Fig. 1f). We wanted to investigate whether this was merely due to the effects of low chick mass, or whether density was also having an additional influence on survival during the post-fledging period. As it was not possible to identify every individual on a post-fledging search, the mean mass of fledged chicks per brood was used in this, and further analyses (see below). There was no difference in the mean weight of chicks per brood between those broods subsequently seen on post-fledging searches and those where adults were located but broods not seen ($t_{43} = -0.07$, $P = 0.95$). There was also no significant relationship between the proportion of chicks in a brood that were seen on post-fledging searches and the mean mass of fledged chicks per brood ($F_{1,42} = 1.81$, $r^2 = 0.04$, $P = 0.19$), suggesting an effect of density on post-fledging survival that is independent of mass at seven days old.

A total of 30 birds individually colour-ringed as chicks (from 20 broods) had been recruited into the breeding population by the end of the 2004 breeding season. Chick weights were compared between broods that supplied recruits to the following year’s breeding populations and

Table 2 Regression analyses relating the change in woodlark breeding density[a] (pairs per hectare of suitable habitat) from year to year to the change in clutch size, mean weight of chicks in a brood, proportion of nestlings that starved, fledging success (chicks per pair) and post-fledging survival (proportion of fledged juveniles that survived the immediate post-fledging period). Data from 2001 to 2002 ($n = 6$ sites) and 2002 to 2003 ($n = 9$ sites)

Variable	*F*	*df*	r^2	*P*
Clutch size	0.31	1.12	0.03	0.59
Mean weight of brood	14.44	1.10	0.59	0.003
% Chicks starved	4.69	1.13	0.27	0.05
Fledging rate	0.12	1.7	0.02	0.74
Post-fledging survival	4.52	1.5	0.48	0.09

[a] The values for change in density were transformed as follows: variable = √[1 + change in density (pairs per hectare)]

those that did not. Only broods known to have survived the post-fledging period were included in the analysis. Those broods that supplied recruits to the local population were significantly heavier than those that did not (Mann–Whitney $U = 89$, $n = 44$, $P < 0.001$). There was no relationship between chick mass at 7 days old and the distance (log transformed) to the subsequent breeding territory ($F_{1,27} = 0.001$, $P = 0.98$), or between density and the rate of recruitment ($F_{1,11} = 0.17$, $P = 0.67$).

Temporal density dependence also operated within sites, between years (Table 2). The mean weight of broods and post-fledging survival all declined significantly as density increased, while the proportion of nestlings that starved increased. There was no significant relationship between the change in density between years and the change in clutch size or fledging success between years.

Discussion

Spatial density dependence can be difficult to measure due to the potentially confounding effect of variation in habitat quality (e.g. Lindström et al. 2005). This study has shown that the shift in distribution in response to recreational disturbance (Mallord et al. 2007a) can be used as a means of studying density dependence as long as the disturbance has no direct demographic impact.

This study has demonstrated that density-dependent processes play a major role in the dynamics of this woodlark population, acting at almost every stage during the breeding season. Clutch size, the weight of chicks at 7 days old, seasonal productivity per pair and post-fledging survival were all negatively related to density (although there was a confounding effect of habitat with clutch size and fledging success). In contrast, the proportion of nestlings that starved increased with density. The most strongly density-dependent breeding stages were nestling starvation (an increase from 0 to ≈50% with density) and post-fledging survival (a decrease from 100 to ≈20% with density). There was a weaker density-dependent effect on clutch size, with about a 25% reduction in the number of eggs laid as density increased. There was, however, no additional density-dependent reduction in brood size at hatching beyond that due to decreased clutch size. However, those first-year birds that were recruited into the population were significantly heavier at 7 days old than other fledglings.

Two often quoted problems preventing identification of density-dependent population processes are appropriate measurements of density (Newton 1998), and the lack of experimental manipulation (Elmberg et al. 2005). That density dependence was successfully detected suggests that, firstly, the measure of density was appropriate. This suggests that the area of *suitable* habitat (in contrast to site area, which would include large tracts of unsuitable habitat) was a pertinent resource for which there would be competition (Elmberg 2003; Lindström et al. 2005). Had we measured density as the number of pairs per site area, including unsuitable habitat, density-dependent relationships would not have been found, and even if they had been, they would not have been valid. Secondly, it also suggests that the novel experimental approach we took was valid, and was not confounded by variation in habitat quality. Had density been determined by site quality, the highest densities would have been found on the best-quality sites (Fretwell and Lucas 1970). Two other lines of evidence support this contention. Firstly, habitat quality was expressly considered in the analyses, by incorporating the area of short grassland (a favoured foraging habitat, which was correlated with density); and secondly, the results of the temporal analyses, in which habitat quality was accounted for by comparing within sites (between years), which (although weaker than the spatial analyses) also showed density-dependent relationships. The strong density relationships suggest that any influence of habitat quality was not sufficient to over-ride the observed density dependence.

There was an apparent relationship between the proportion of short grassland on a site and clutch size, which removed the significant negative effect of density on clutch size. Areas of grassland could be providing females with a particular resource prior to egg laying. However, although woodlarks occur at low density on sites with large grass fields, large parts of these fields remained unused; therefore, the apparent importance of grassland may result from the negative correlation between the proportion of grassland and density. The relationship between density and fledging success is also non-significant, perhaps due to the way that density has been measured. Low density can occur if there is only one pair on a site with a reasonable amount of suitable habitat, or where there are many pairs on a very large amount of habitat. In the first case if the single pairs are predated, then the per-site fledging success is zero, thus such sites add stochastic error to the test of density dependence. Conversely, on sites with many pairs, the productivity of other pairs dampens the effect of the complete failure of individual pairs.

Density per se is unlikely to be the direct cause of demographic variation, often acting instead by increasing competition for a limited resource, particularly food. Supplementary-feeding experiments have often demonstrated increases in clutch size, nestling weight and fledging success (e.g. Arcese and Smith 1988; Ewald and Rohwer 1982; Högstedt 1981; Newton 1998), all parameters shown to be density-dependent in this study.

The effect of density on chick mass has potentially far-reaching consequences. Many studies have shown that nestling mass is a good predictor of subsequent juvenile survival (e.g. Magrath 1991; Both et al. 1999; Perrins and McCleery 2001; Menu et al. 2005). The immediate post-fledging period is often thought to be the most critical period for juvenile survival in passerine birds (Magrath 1991; Naef-Daenzer et al. 2001; Sullivan 1989). We have shown in this study that survival of recently fledged woodlarks during this period is strongly density dependent; however, there was no significant trend in the proportion of chicks in a brood that survived as the mean weight of fledged chicks per brood increased. This suggests that it is not just the condition of birds at fledging that influences the high subsequent mortality, but that density is also acting independently during the post-fledging period, when juveniles are still dependent on the parental territory.

Given the strong effect of density on chick mass, food may also be limiting in the post-fledging period. Food limitation and starvation have only rarely been cited as important factors causing post-fledging mortality (e.g. Magrath 1991), although Sullivan (1989) found that juvenile yellow-eyed juncos *Junco phaenotus* often starved immediately after becoming independent from their parents. Sites with higher densities of woodlarks did not have higher abundance of major predators (carrion crows *Corvus corone*, magpies *Pica pica* and red foxes *Vulpes vulpes*; J. Mallord, unpublished data). Thus, it seems likely that the greater rates of post-fledging mortality at higher densities are due to food shortages, or their interaction with predation on hungry juveniles (Green and Cockburn 2001; Naef-Daenzer et al. 2001; Sullivan 1989).

That starvation of nestlings explained much of the variation in productivity between sites, that starvation itself was strongly related to the weight of nestlings at 7 days old, and that there was large variation in chick weights, all suggest that food limitation was the driving force behind all the density-dependent relationships found in this study. This is perhaps not surprising as there was a 20-fold difference in density and hence in the area of suitable habitat available to each pair, which varied from 16.67 to 0.85 ha per pair in 2003.

Although we did not find a direct effect of density on recruitment, the mass of woodlark chicks at 7 days old appears to be important in determining whether juveniles survive from the post-fledging period to be recruited into the breeding population. Similarly, other studies (e.g. Both et al. 1999; Magrath 1991) also found that heavier chicks are more likely to be recruited into the breeding population. As woodlark juveniles leave their natal sites after independence, it is not known whether most mortality occurred immediately after independence (e.g. Magrath 1991; Tinbergen and Boerlijst 1990), or later in the winter.

Measurements of recruitment can be biased by dispersal out of the study area (e.g. Lambrechts et al. 2000). In the present study this could be a problem if there were differences in dispersal tendencies according to nestling weight (e.g. Drent 1984). However, known natal dispersal distances in the Dorset woodlark population were short (c75% of birds travelled ≤ 4 km, Mallord 2005), and there was no correlation between chick mass and dispersal distance. Another potential bias is that lighter birds may be less likely to obtain a territory, although again the evidence for this is inconclusive (e.g. Perrins and McCleery 2001; Reynolds 1997). In the present study, birds are only found when they are territory holders, so it is not possible to comment on the existence, or otherwise, of a non-breeding population, and whether it consists of birds in poorer condition.

Although the loss of heathlands has slowed in recent decades (Rose et al. 2000), habitat succession (Bowden 1990) and increasing pressure from human recreation (Haskins 2000; Mallord et al. 2007a) could negatively impact upon the woodlark population. There is always much debate between conservationists and those proposing an alternate land use as to the impact of such changes on wildlife populations (Sutherland and Norris 2002) and the extent to which population responses are dependent on the strength of density dependence (Sutherland 1998). Understanding the strength and form of density dependence allows predictions to be made as to the effect on the population of habitat loss or degradation. Appreciating the spatial nature of the effects of density can give a better understanding of how to manage such populations.

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