Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines

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Agricultural intensification is believed to have driven declines of farmland bird populations and the invertebrates and weeds on which they feed. We investigated whether habitat and weather, as surrogates for food availability, influenced nestling growth rates and condition of four farmland passerines (Skylark *Alauda arvensis*, Chaffinch *Fringilla coelebs*, Linnet *Carduelis cannabina* and Yellowhammer *Emberiza citrinella*). We also tested whether nestling growth rates or condition influenced whether a brood subsequently fledged, starved or was depredated. Linnet nestlings are fed almost exclusively on seeds, and were unaffected by weather. Nestlings of the other species are fed mainly invertebrates and were affected negatively by rain but positively by increasing minimum temperatures and daily hours of sunshine. Condition and growth rates of Linnet nestlings were lower in nests further from oilseed-rape fields, rape seeds being important in the diet of this species. Nestlings of the other three species were unaffected by availability of habitats selected by parents foraging for nestling food. Brood fate was not influenced by growth rates or condition for any species. Most models explained little variation in the response variable. Possible reasons, including the possibility that parents trade off their own survival prospects to ensure reproductive success, are discussed.

Recent declines in farmland bird populations in north-west Europe are very well documented (Tucker & Heath 1994, Fuller *et al.* 1995, Gregory *et al.* 2001). That agricultural land-use change has played at least some part in these declines now seems beyond doubt (Krebs *et al.* 1999, Fuller 2000, Donald *et al.* 2001a). Recent changes in agricultural land-use and crop management have also been correlated with severe and widespread declines in many farmland invertebrates and weeds on which birds feed (Wilson *et al.* 1999, Sotherton & Self 2000). Yet the effect of food availability on breeding success has been proven to have contributed to population decline for only one farmland bird species in the UK. The Grey Partridge *Perdix perdix* has declined in part because of the effect of pesticides on the availability of chick-food invertebrates in cereal crops (e.g. Potts &

Aebischer 1995). For many passerine species there is no evidence of a decline in 'per-nest' measures of reproductive output over the period of population decline (e.g. Siriwardena *et al.* 2000a), although numbers of breeding attempts may have fallen (e.g. Skylarks: Donald & Vickery 2000). Falls in survival rate are more often a correlate of decline (e.g. Siriwardena *et al.* 1998, 1999, Peach *et al.* 1999).

Alternatively, as reproductive success is determined by the successful recruitment and breeding of offspring, it may be reduced if parents maintain offspring quantity at the expense of offspring quality. Nestling body condition is often a correlate of future survival rates, social status and even lifetime reproductive success (e.g. Magrath 1991, Hochachka & Smith 1991, Lindström 1999). Poor condition can also lead to increased begging (Cotton *et al.* 1996), which could attract predators and lead to state-dependent predation (Evans *et al.* 1997). Given reductions in their food, it is plausible that farmland

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birds may be suffering reduced nestling condition and/or growth rates, as a result of either lowered intake rates or a diet dominated by less profitable food items (Borg & Toft 2000).

One hypothesis for the apparent lack of effect of declining breeding season food availability on the reproductive success of farmland passerines is that parent birds may absorb the impacts of a deteriorating environment by working harder in order to maintain reproductive output at the cost of a reduction in their own survival (Leugger-Eggimann 1997, Richner & Tripet 1999, Forbes & Mock 2000). In short-lived passerine birds, where many individuals may have only one breeding opportunity in their lifetime, this strategy is more likely than in longer-lived species where birds may simply not breed in poor conditions (Clutton-Brock 1988).

Experimental studies of Collared Flycatchers *Ficedula albicollis* and Barn Swallows *Hirundo rustica* have shown both that reproduction has survival costs to parents and that parents may balance offspring quality against their own survival prospects (e.g. Gustafsson & Sutherland 1988; Saino *et al.* 1998). This hypothesis therefore predicts weak correlations between variation in breeding habitat quality and measures of nestling growth, condition and reproductive success, because the effects of environmental variation are absorbed primarily by the parent birds, potentially at the cost of their own survival prospects. The same prediction arises from the hypothesis that breeding season food supplies remain non-limiting, despite recent agricultural intensification. Alternatively, if variation in breeding habitat quality does limit reproductive output and if this variation is not compensated for by parental effort, then we should expect to see strong correlations between environmental variation and variation in nestling growth, condition and overall reproductive success.

We examined the strength of correlations between habitat and weather variables, and nestling condition, growth rate and the probability of subsequent brood survival to fledging for four farmland bird species (Skylark *Alauda arvensis*, Chaffinch *Fringilla coelebs*, Linnet *Carduelis cannabina* and Yellowhammer *Emberiza citrinella*). Previous studies have already shown that overall measures of reproductive success such as clutch size and brood size are not generally correlated strongly with local habitat variation in these species (e.g. Wilson *et al.* 1997, Bradbury *et al.* 2000, Moorcroft 2000, Whittingham *et al.* 2001), although there are some effects of broader farm-type (pastoral, arable or mixed: Siriwardena *et al.* 2000b).

For the Linnet, the influence of variation in nestling diet was also tested because this can be quantified when the nestlings are handled (see Methods). In the UK, the Skylark has been in population decline since the mid-1970s, the Chaffinch population has remained relatively stable, the Linnet population declined steeply from the early 1960s to the late 1980s, and the Yellowhammer has been in steep decline since the late 1980s (Gregory *et al.* 2001).

METHODS

Study sites and biometric data collection

The study was carried out from April to July in 1994–99, at nine lowland farms in Oxfordshire, Wiltshire and Warwickshire, UK. Land-use and management at these sites has been described elsewhere (Wilson *et al.* 1997, Bradbury *et al.* 2000). For Skylark, Chaffinch and Yellowhammer, fieldworkers found territories using Common Birds Census methods (Marchant *et al.* 1990), and then found nests by watching for signs of breeding behaviour. For Linnets, which are not territorial, nests were found by direct observation of nesting behaviour (Moorcroft & Wilson 2000). Nestlings were weighed (to the nearest 0.1 g) using a Pesola spring balance and their tarsus length – from the depression in the angle of the intertarsal joint to the end of the folded foot – was measured using dial calipers (to the nearest 0.1 mm). The age, in days, of the nestlings was known from the date of hatch or, when this was not known, was estimated by comparison of feather development with known-age broods.

Predictor variables

Habitat and diet data

Measures of habitat known to be selected or avoided by adult birds during territory settlement, or when foraging for nestling food (Table 1), were recorded as surrogates of food availability. It would have been ideal to measure food availability directly within each territory, but logistically this was beyond the scope of this study.

For Skylark, the crop type of the field in which a nest is located and farm 'type' (organic or conventional management: see Wilson *et al.* 1997, Bradbury *et al.* 2000) can both influence the structure of the sward and invertebrate abundance, which interact to determine the availability of food resources (Odderskaer *et al.* 1997).

Table 1. Predictor variables entered into the analysis of variation in condition and growth rates. Species denotes the species for which the term was entered into the full model (S, Skylark; C, Chaffinch; L, Linnet; Y, Yellowhammer). Dandelion grass is grass suitable for dandelion growth (permanent pasture, roadside verges). Non-dandelion grass is grass unsuitable for dandelion growth (silage, hay, new grass leys, wide grass field margins). In practice, variables that were 'next to nest' were always within 10 m of the nest.

Predictor	Type	Species	Description	Reference
Year	Factor	S,C,L,Y		
Date	Continuous	S,C,L,Y	Of measure (condition); mid-point between measures (growth)	
Brood size	Continuous	S,C,L,Y		
Max. dry bulb temp.	Continuous	S,C,L,Y	in °C, over 24 h, from 09:00 h on the day of interest	
Min. dry bulb temp.	Continuous	S,C,L,Y	in °C, over 24 h, to 09:00 h on the day of interest	
Precipitation	Continuous	S,C,L,Y	in mm, from 00:00 to 24:00 h on the day of interest	
Sunshine hours	Continuous	S,C,Y	from 00:00 to 24:00 h on the day of interest	
Farm-type	Factor	S,C,L,Y	Intensive (1), organic (2)	Campbell and Cooke (1997)
Crop-type	Factor	S	Winter cereal (1), spring cereal or linseed (2), set aside (3), silage (4)	
Field area	Continuous	S		Wilson (2001)
'Boundary index'	Continuous	S		Wilson et al. (1997)
Oak trees	Factor	C	Absent (1), present (2), dominant (3); in hedge containing nest	Whittingham et al. (2001)
Woody plant species	Continuous	C	Number of species in the hedge containing nest, per 10 m	Whittingham et al. (2001)
Distance to wood	Continuous	C	Distance (m) to nearest woodland block	Whittingham et al. (2001)
Chaffinch habitat	Factor	C	Grass fields surround nest (1); both grass and arable fields around nest (2); arable fields surround nest (3)	Whittingham et al. (2001)
Distance to rape	Continuous	L	Nearest straight-line distance from nest to rape field	Moorcroft (2000); Moorcroft and Wilson (2000)
'Dgrass' adjacent	Factor	L	'Dandelion-grass' next to nest (1) or not (0)	Moorcroft (2000); Moorcroft and Wilson (2000)
'Ndgrass' adjacent	Factor	L	'Non-dandelion-grass' next to nest (1) or not (0)	Moorcroft (2000); Moorcroft and Wilson (2000)
Track	Factor	L	Track next to nest (1) or not (0)	Moorcroft (2000); Moorcroft and Wilson (2000)
Gullet rape	Continuous	L	Proportion of seed volume occupied by rape	Moorcroft (2000); Moorcroft and Wilson (2000)
Gullet dandelion	Continuous	L	Proportion of seed volume occupied by dandelion	Moorcroft (2000); Moorcroft and Wilson (2000)
Gullet Stellaria	Continuous	L	Proportion of seed volume occupied by *Stellaria* or *Capsella*	Moorcroft (2000); Moorcroft and Wilson (2000)
Gullet other	Continuous	L	Proportion of seed volume occupied by other seed species	Moorcroft (2000); Moorcroft and Wilson (2000)
Yellowhammer habitat	Factor	Y	Grass fields surround nest (1); arable fields next to nest (2)	Bradbury et al. (2000); Morris et al. (2001)
Max. strip width	Continuous	Y	Maximum width (m) of uncropped field margin next to nest	Bradbury et al. (2000); Morris et al. (2001)

Yellowhammers forage preferentially for nestling food in rough field margins (Morris *et al.* 2001), while avoiding grass fields. Rough field margins support high densities of invertebrates (e.g. Dennis *et al.* 1994), while modern management of pasture and grass leys is inimical to most non-soil invertebrates (Fuller 2000). The availability of margin habitat to nests and whether or not the nest was surrounded by grass fields were therefore used as predictors of food availability for Yellowhammers.

Chaffinches on farmland feed mainly on defoliating caterpillars (Newton 1967) and territory dispersion can be correlated with the availability of features that support these prey (Whittingham *et al.* 2001). Such features (e.g. distance to woodland, availability of oak trees and plant species diversity in the hedge in which the nest was located) were therefore included as predictors of food availability.

The young of most farmland bird species have an invertebrate diet (Wilson *et al.* 1999), but Linnets, as in other *Carduelis* species, feed nestlings extensively on a diet of partially ripe seed (Newton 1967). Cardueline finches store food in a gullet that is covered by semitransparent skin, so diet composition can be recorded as the percentage of total seed volume occupied by each seed type (Moorcroft *et al.* 1997). To assess the effect of diet components on nestling development, log-ratio transformations of these percentages were used as predictor variables in the models, with data from individual nestlings pooled to give brood means. However, chick development will be determined not only by the nature of the food eaten, but also by the effort needed to collect that food (via parental visit rates to the nest). Moorcroft *et al.* (1997) have shown that Linnets at our study sites feed primarily on dandelion *Taraxacum* spp. and oilseed rape *Brassica napus* seeds. The effects on chick development of availability of rape and dandelion were therefore modelled using distance to rape field and proximity to the nest of habitat features that support dandelions. 'Dandelion grass' and 'non-dandelion grass' features were either whole fields next to the nest (e.g. pasture, silage ley, hay) or linear features (track or grass margin) at least 1 m wide running the entire length of the field boundary in which the nest was located.

Weather data

Daily weather data were obtained with permission from the archive of the British Atmospheric Data Centre (BADC) and were extracted from the climate station closest to each study site. Four weather variables were extracted (Table 1). Precipitation data were ($\ln x + 1$) transformed. For analysis of condition, the mean daily value for each of these weather variables was calculated over the lifetime of the brood. For analysis of growth rates, the mean daily value was calculated between the days of the two measurements inclusive. All four weather variables were used for analyses of Skylark, Chaffinch and Yellowhammer data. 'Sunshine hours' was not used in the analyses of Linnet data, as it is unlikely to affect short-term seed availability.

Other variables

Year of study, brood size and date were also included as predictor variables to control for expected variation caused by these variables (Table 1).

Data analysis

Nestling condition

Measurements of mass and tarsus length were taken from most broods on several days. In order to avoid pseudoreplication in the analysis of condition, data from only one day were used for each brood. We chose the last measurement made of each brood. This maximized the chance of detecting cumulative environmental effects on condition and also provided a measurement that was closest to condition at fledging, which should be most pertinent to the effects of fledgling quality on future fitness.

The condition of each nestling was estimated as its residual from the regression of the natural logarithm of mass on the natural logarithm of size (Jakob *et al.* 1996), here measured as tarsus length. Natural logarithms (ln) were used to account for the probable allometric relationship between a measure of mass and a measure of length, i.e. mass = a (tarsus^b). As the last measurements of different broods were taken over a small spread of nestling ages, we had to control for possible effects of nestling age on condition index. Hence, we first included nestling age and the interaction term between nestling age and ln tarsus as predictors of ln mass. If the interaction term had a significant effect on ln mass, then the residuals of this analysis, which were independent of nestling age, were used as measures of condition. If the interaction was not significant, then the residuals of a regression of ln mass on ln tarsus were used as measures of body condition.

Although data were collected from all nestlings within all broods, siblings within broods are clearly not independent in any statistical analysis because

they are fed by the same parents and experience the same ambient conditions. Variation in the mean condition index of each brood was therefore analysed as a function of the predictor variables. In order to detect any more subtle effects that had been masked by the brood mean, variation in the condition index of the nestling with the poorest condition in each brood was also analysed in a separate analysis (Nilsson & Gårdmark 2001).

The analysis was simplified by excluding any broods in which there was brood reduction prior to the measurement used to calculate the condition index. Brood reduction could complicate the analysis for two reasons. First, assuming that the nestlings that die are those in poorest condition, brood mean condition will immediately be inflated relative to unreduced broods. Secondly, the remaining nestlings may be able to respond to the reduced sibling competition by increasing condition or growth rates, again inflating these measures relative to unaffected broods (Shkedy & Safriel 1992).

Growth rates

We calculated daily rates of growth of tarsus (TGR) and body mass (MGR) using only those intervals between measurements within the linear phase of growth. As determined by eye from a plot of tarsus or mass against age, the 'linear' period fell between ages 3–8 days post-hatching for Skylarks, 3–8 for Chaffinches, 4–8 for Linnets and 1–7 for Yellowhammers. If more than two measurements had been taken from a brood within this period, the two measurements covering the maximum span of days were used. The resulting growth rate, in grams of mass or millimetres of tarsus gained per day, was assigned the age of the nestlings at the mid-point between the two measurements (Donald *et al.* 2001b). In case the relationship between growth rate and nestling age was not accounted for satisfactorily by assuming a linear relationship, we then controlled for any remaining effect of nestling age by including age as a predictor in the analysis. Analyses were again performed on two measures: (a) the mean growth rate for each brood and (b) chicks with the smallest growth rate in each brood. Any broods in which there was brood reduction prior to the first measurement or between the first and second measurements were again excluded from analysis.

Modelling correlates of nestling growth and condition

MINITAB release 12 (Minitab 1998) was used to test for significant correlates of variation in growth rate and condition, specifying normal errors. First, a full model was constructed, with all predictor variables included (Table 1). Quadratic terms were included to test for simple curvilinear effects. A step-down deletion procedure was used to establish the minimum adequate model (MAM: Crawley 1993). Inspection of the data revealed that, for all species, some weather variables were highly correlated. Hence, if a weather variable excluded from the MAM was found to be highly correlated with another weather variable retained in the MAM, alternative MAMs were constructed (in the event, no 'alternative' weather variables had a significant effect when substituted into the MAM).

In order to control for unmeasured variation between sites, a variable 'farm' (nine levels, identifying the nine study sites), was added into the MAMs. Predictor variables becoming non-significant once 'farm' was introduced were more likely to vary between rather than within farms; their effects were interpreted with this in mind, because such variables are the most likely to have been acting as surrogates for other, unmeasured variables acting at the farm level (Bradbury *et al.* 2000).

Effects of nestling condition and growth rates on brood fate

Nominal logistic regression was used to test whether nestling condition or growth rates influenced brood fate. Brood fate was designated one of three outcomes; all nestlings fledged, all nestlings starved and all nestlings depredated. To maximize the differential between fates, cases where some nestlings fledged and some starved were excluded from the analysis, as this 'event' was considered intermediate between 'all fledged' and 'all starved'. Where significant results were found, binary logistic regression was used to test for significant pairwise differences in condition or growth rates between different brood fates. In addition, to test whether variation in growth or condition influenced partial brood losses, we also examined their effects on the proportion of hatched nestlings that fledged. This was evaluated using binomial logistic regression, with number of nestlings fledged as the response variable and number hatched as the binomial denominator, for all species except Skylark. Skylarks leave the nest 'early' (they are then cursorial for several days before they can fledge properly), so it is impossible to determine accurately how many birds survived to fledging.

RESULTS

Skylark

Nestling body condition and growth rates (summarized from Table 2a)

The habitat variables measured showed no effect on either condition index or growth rate. Condition index decreased with increasing maximum temperature and increased with increasing minimum temperature. MGR and TGR showed a quadratic response to minimum temperature, peaking at intermediate values. Increasing hours of sunshine were associated with lower TGR, but higher condition index. The proportion of variance explained varied from 0 to 6.4% for condition index and from 9.7 to 26.2% for growth rates.

Effects of condition and growth rates on survival to fledging

Brood fate was influenced significantly by both mean condition index ($G_2 = 13.52$, $P = 0.001$) and MGR ($G_2 = 21.17$, $P < 0.001$), but not by TGR ($G_2 = 3.96$, $P = 0.138$). Broods which later suffered starvation had significantly lower condition indices ($G_1 = 11.38$, $P = 0.001$) and MGR ($G_1 = 20.70$, $P < 0.001$) than those that fledged, as well as having significantly lower condition indices ($G_1 = 7.82$, $P = 0.005$) and MGR ($G_1 = 7.11$, $P < 0.008$) than those that were subsequently depredated. There was no difference in condition index ($G_1 = 0.94$, $P = 0.333$) or MGR ($G_1 = 0.44$, $P = 0.508$) between broods that went on to fledge and those that went on to be depredated.

Chaffinch

Nestling body condition and growth rates (summarized from Table 2b)

Only 29 broods conformed to the requirements of our growth rate analyses. This was considered insufficient for a full multivariate analysis. In univariate tests, none of the putative predictor variables had a significant effect on growth rate (for brevity, these results are omitted here). Nestling condition was not associated with any of the habitat or weather variables measured, but decreased with increasing brood size. The proportion of variance explained by the univariate tests and MAM varied from 6.4 to 13.6%.

Effects of condition on survival to fledging

There was a highly significant effect of mean condition index on brood fate ($G_2 = 13.073$, $P = 0.001$).

Broods that later starved were in significantly worse condition than either those that fledged ($G_1 = 12.231$, $P < 0.001$) or those that were subsequently depredated ($G_1 = 9.613$, $P = 0.002$). There was no difference in condition between broods that went on to fledge and those that went on to be depredated ($G_1 = 0.012$, $P = 0.912$). There was no effect of condition on subsequent partial brood loss ($G_1 = 0.364$, $P = 0.547$).

Linnet

Nestling body condition and growth rates (summarized from Table 2c)

Condition index, TGR and MGR were all lower in broods further from oilseed-rape fields. There were no significant effects of any weather or diet variables on condition index or growth rate. Condition index of lowest-ranked nestlings decreased during the season. The proportion of variance explained by the models varied from 6.1 to 9.6% for condition index and (not including the effect of nestling age) 0–2.8% for growth rates. The inclusion of 'farm' weakened the relationship between MGR/condition index and distance to rape fields.

Effects of condition and growth rates on survival to fledging

Brood fate was not influenced by mean body condition ($G_2 = 4.57$, $P = 0.101$), TGR ($G_2 = 0.504$, $P = 0.777$) or MGR ($G_2 = 3.592$, $P = 0.166$). When successful and depredated broods were pooled, these together had higher condition indices ($G_1 = 3.969$, $P = 0.046$) and nearly significantly faster MGR ($G_1 = 3.611$, $P = 0.057$), but not TGR ($G_1 = 0.242$, $P = 0.622$), than starved broods. There was no effect of condition on subsequent partial brood loss ($G_1 = 0.327$, $P = 0.567$). There was no partial brood loss subsequent to the last measurement of broods used for the growth analysis.

Yellowhammer

Nestling body condition and growth rates (summarized from Table 2d)

Neither condition nor growth rate was associated with any of the habitat variables measured. Condition index decreased with increasing maximum temperature, while both TGR and MGR decreased with increasing precipitation. Larger broods had lower condition indices and MGR of lowest-ranked nestlings. The proportion of variance explained by all models varied from 7.1 to 14.1% for condition

Table 2. Significant predictors, including square terms, of nestling body condition index and growth rates (* = displaced from MAM by addition of farm factor). R^2 are partial R^2 for each variable in the MAM, with total R^2 for the MAM given in italics below.

		F-value	P-value	R^2 (%)	Coefficient
(a) Skylark					
Mean condition	Max. temperature	$F_{1,98} = 6.72$	0.011	6.42	−0.0236
	Min. temperature	$F_{1,98} = 5.05$	0.027	4.82	0.0229
	Sunshine hours	$F_{1,98} = 4.17$	0.044	3.98	0.0175
				6.44	
Min condition	–	–	–	–	–
Mean tarsus	Min. temperature	$F_{1,72} = 10.24$	0.002	10.50	0.3030
	Min. temperature^2	$F_{1,72} = 12.59$	0.001	12.90	−0.0179
	Sunshine hours	$F_{1,72} = 8.65$	0.004	8.86	−0.0765
				26.2	
Min tarsus	Min. temperature	$F_{1,72} = 4.92$	0.03	5.65	0.2443
	Min. temperature^2	$F_{1,72} = 4.18$	0.045	4.80	−0.1447
	Sunshine hours	$F_{1,72} = 8.63$	0.004	9.91	−0.0737
				17.36	
Mean mass	Min. temperature	$F_{1,73} = 10.99$	0.001	13.07	0.5974
	Min. temperature^2	$F_{1,73} = 9.78$	0.003	11.63	−0.0361
				13.19	
Min mass	Min. temperature	$F_{1,73} = 7.81$	0.007	9.67	0.5217
	Min. temperature^2	$F_{1,73} = 7.35$	0.008	9.09	−0.0324
				9.67	
(b) Chaffinch					
Mean condition	Brood size	$F_{1,66} = 4.44$	0.039	6.40	−0.0263
Min condition	Brood size	$F_{1,66} = 10.22$	0.002	13.59	−0.0418
(c) Linnet					
Mean condition	Year	$F_{3,309} = 7.60$	<0.001	8.57	–
	Distance to rape*	$F_{1,309} = 10.11$	0.002	3.80	–
				9.61	0.00005
Min condition	Year	$F_{3,309} = 4.73$	0.003	4.37	–
	Date	$F_{1,309} = 5.45$	0.020	1.68	−0.0007
				6.08	
Mean tarsus	Distance to rape	$F_{1,162} = 4.82$	0.030	2.56	−0.0001
	Nestling age	$F_{6,162} = 4.71$	<0.001′	15.04	–
				17.96	
Min tarsus	–	–	–	–	–
Mean mass	Distance to rape*	$F_{1,162} = 4.60$	0.034	2.78	−0.0002
Min mass	–	–	–	–	–
(d) Yellowhammer					
Mean condition	Brood size	$F_{1,211} = 13.12$	<0.001	5.79	−0.0266
	Max. temperature	$F_{1,211} = 4.48$	0.035	1.98	−0.0040
				7.07	
Min condition	Brood size	$F_{1,211} = 34.27$	<0.001	14.07	−0.0524
Mean tarsus	Nestling age	$F_{10,104} = 3.26$	0.001	24.99	–
	Precipitation	$F_{1,104} = 4.93$	0.029	3.78	−0.4622
				29.72	
Min tarsus	Nestling age	$F_{10,104} = 4.48$	<0.001	30.85	–
	Precipitation*	$F_{1,104} = 7.37$	0.008	5.07	−0.6271
				37.03	
Mean mass	Precipitation	$F_{1,104} = 4.33$*	0.040	4.03	−0.7895
Min mass	Brood size	$F_{1,104} = 7.10$	0.009	6.19	−0.2855
	Precipitation	$F_{1,104} = 5.63$	0.020	4.90	−1.0129
				11.80	

index, and (when discounting nestling age) from 3.8 to 5.1% for growth rates.

Effects of condition and growth rates on survival to fledging

Brood fate was not influenced significantly by mean body condition index ($G_2 = 3.552$, $P = 0.169$), TGR ($G_2 = 0.262$, $P = 0.877$) or MGR ($G_2 = 4.420$, $P = 0.110$). However, when successful and depredated broods were pooled, these together had near-significantly higher condition indices ($G_1 = 3.462$, $P = 0.063$) and significantly faster MGR ($G_1 = 4.206$, $P = 0.040$), but not TGR ($G_1 = 0.139$, $P = 0.709$) than starved broods. There was no effect on subsequent partial brood loss of condition ($G_1 = 2.383$, $P = 0.123$) or TGR ($G_1 = 1.312$, $P = 0.252$), although the proportion of hatchlings that fledged increased with increasing MGR ($G_1 = 6.718$, $P = 0.010$).

DISCUSSION

Effects of habitat availability

For Linnet, condition index, TGR and MGR were all lower in nests further away from oilseed-rape fields. When arable weed seeds are limited, Linnets are highly dependent on unripe rape seed as a food source for nestlings (Moorcroft *et al.* 1997) and the number of nestlings fledged is higher in nests nearer to rape fields (Moorcroft 2000). However, there was no relationship between the amount of rape seed in the gullet and the distance to a rape field (Fig. 1). Taken together, these results may suggest that Linnets are prepared to fly very large distances to collect the favoured food item, rape seed, perhaps at a cost of lower provisioning rates, which would have knock-on effects on nestling condition, growth rate and survival. Unfortunately, we do not have data on provisioning rates to test this prediction. It is therefore possible that rape availability enhances not only the productivity of Linnets, but also the quality of offspring produced. Indeed, Linnet nestlings reared in a predominantly arable farming system without rape are in consistently poorer condition than those in a farming system with rape (Moorcroft 2000). Moreover, in maintaining provision of rape seed, despite distance to the source of that food, Linnets may be working harder and thereby compromising their own survival prospects (Leugger-Eggimann 1997, see Conclusion).

Farm tracks, roads and pasture fields are the main providers of dandelions, the other dominant Linnet
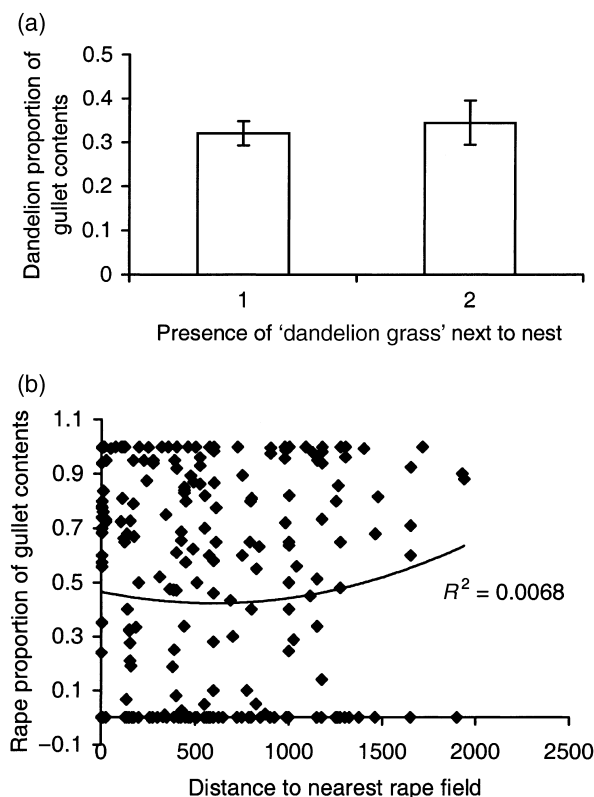

Figure 1. The lack of relationship between proportion of gullet contents comprising key food items and availability of those food items. (a) Histogram demonstrating relationship between proportion of gullet content comprising dandelion seeds and whether the nest was adjacent to a habitat which promoted dandelion growth (2) or not (1). (b) Scatter plot demonstrating relationship between proportion of gullet content comprising rape seeds and distance to nearest rape field.

nestling food (Moorcroft *et al.* 1997), and yet the proximity of these features to the nest did not influence condition or growth rates. One explanation may be that the measure of availability of these habitats was inappropriate. These weeds are typically found in highly dispersed, yet spatially clumped, distributions, and parent Linnets will fly up to 2 km to find food for their nestlings (Moorcroft 2000). Thus, proximity of these habitats to the nest may be relatively unimportant in comparison to their availability at a wider spatial scale.

The other three species were not affected by local habitat variation that is known to be associated with patterns of territory settlement, nest location and foraging habitat selection. Crop-type and farm-type (organic or conventional intensive) influence crop management and pesticide load, which in turn affects invertebrate abundance both directly, through mortality, and indirectly, through removal

of weed food-plants (Campbell & Cooke 1997, Elmegaard *et al.* 1999). Therefore, for Skylark, both crop- and farm-type would be expected to influence prey availability and hence nestling condition (Donald *et al.* 2001b), yet neither did so in this study. Chaffinches on farmland feed mainly in trees, predominantly oaks, when searching for food such as defoliating caterpillars (Newton 1967, Whittingham *et al.* 2001), and yet availability of solitary oaks or woodland blocks had no impact on nestling development. Yellowhammers avoid grass fields and select arable field margin strips, which support high densities of invertebrate food (e.g. Dennis *et al.* 1994), both during settlement (Bradbury *et al.* 2000), and when foraging for nestling food (Morris *et al.* 2001), and yet no effect on nestling development was observed of the proximity of these habitats.

It is possible, for Skylark, Chaffinch and Yellowhammer, that effects were not seen because, as perhaps for some of the Linnet habitats, habitat availability was measured inappropriately, perhaps at the wrong spatial scale. Alternatively, the most important environmental predictors may not have been measured. In particular, we were not able to measure the availability of food in individual territories directly, and habitat availability *per se* might not reflect real resource availability. A final possibility is that birds simply did not settle in low-quality habitat, though the variation described in Appendix 1 would suggest that this is not the case.

Effects of weather

Weather could affect nestling development in at least three ways, which could all interact. These effects act both directly on the birds themselves, and indirectly on the food supply (McCarty & Winkler 1999). First, lower temperatures and high rainfall could both chill nestlings and hence increase their energy demands for thermoregulation, reducing the availability of resources for development. Secondly, by increasing thermoregulatory demands, low temperatures and high rainfall could reduce nestling development by reducing feeding time for the female (who must brood the nestlings to keep them warm and dry) and hence reducing intake rates. Thirdly, low temperatures, high rainfall and reduced sunshine hours could all reduce invertebrate activity and hence availability, leading to lowered intake rates.

The negative effect of precipitation on TGR and MGR of Yellowhammers is consistent both with thermoregulatory costs, and with reductions in invertebrate availability. In warmer conditions, thermoregulatory costs decrease and invertebrate availability increases. Invertebrate activity, and therefore availability, should also increase with increasing hours of sunshine. This may explain why the Skylark condition index increased with both increasing minimum temperature and increasing hours of sunshine. However, both Skylark and Yellowhammer show a negative relationship between increasing maximum temperature and nestling condition. In hot conditions during the day, nestlings may be investing energy in heat dissipation and parents may spend more time brooding to shade nestlings, thus reducing food intake rates (J. D. Wilson unpubl. data).

Lack of starvation-mediated predation

In Cirl Buntings *Emberiza cirlus*, broods in successful nests had significantly higher MGR than both those that were predated and those that suffered starvation (Evans *et al.* 1997). It was suggested that the lack of a significant difference in condition between starved and predated broods was the consequence of starvation-mediated predation. That is, in times of food shortage, increased sibling competition resulting from hunger may increase begging intensity, making broods more vulnerable to predation (Haskell 1994, Evans *et al.* 1997). In none of the species in this study did depredated broods have significantly poorer condition or lower growth rates than successful broods. These results suggest that predation in these species may not be enhanced by starvation and so is not state-dependent.

CONCLUSIONS

For all four species, almost all the models explained only a small proportion of variance in condition and growth rates (a maximum of 26% for Skylark nestling growth rates). This result is consistent with the hypothesis that parents may be compensating for spatial (i.e. food availability within the foraging range) and temporal (i.e. weather-induced) variations in habitat quality in order to maintain the number and quality of nestlings fledged. This has been seen in Red-backed Shrikes *Lanius collurio*, where birds breeding in high-intensity farming areas managed to produce the same number of chicks as in

low-intensity areas, but the chicks were lighter, and the adults had to invest more time in flight activity (energy expenditure) and had lower weights (Leugger-Eggimann 1997). If such compensation is taking place in the present study, then the effects of a deterioration in quality of breeding habitat may be translated into impacts on the number of nesting attempts per season or survival rates of fully grown birds, rather than being reflected directly in reduced breeding output per breeding attempt. This, in turn, is consistent with the observation that survival rates of declining farmland passerines have tended to fall during the period of population decline whilst measures of 'per-attempt' reproductive success have not done so (Siriwardena *et al.* 2000a).

Of course, this simple correlative study cannot provide all the answers because there are other possible explanations for the results observed. Habitat availability may not have been (a) a direct measure of resource availability, and (b) measured at the appropriate spatial scale, and despite decreases in nestling food availability (Sotherton & Self 2000), breeding season food availability may not be the most limiting resource. Despite reductions, breeding season resources may not be limiting, simply because reductions in other resources (e.g. winter seed food availability) have been greater and are more limiting to the population (Bradbury *et al.* 2001). Alternatively, observations of increasing reproductive success during periods of population decline (Siriwardena *et al.* 2000a) may reflect a density-dependent response to declines caused by a more limiting factor such as winter food.

Although experimental studies will be needed to test these alternative hypotheses, this study does demonstrate that variations in nestling condition and growth rate amongst farmland passerine birds are not well explained simply by local environmental variation. A fuller understanding of the causes of decline of many of these species depends on understanding why this is so.

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APPENDIX 1.

Variability of variables given in Table 1. For factors, number of occurrences of each factor level is given.

	Condition analysis	Growth rate analysis
Skylark		
Crop type	1 = 25; 2 = 16; 3 = 34; 4 = 22	1 = 20; 2 = 14; 3 = 24; 4 = 13
Chaffinch		
Oak trees (three levels)	1 = 34; 2 = 17; 3 = 16	
Woody plant species (c)	Median = 0.361; IQR = 0.387	
Distance to wood (c)	Median = 470 m; IQR = 355 m	
Habitat (three levels)	1 = 17; 2 = 15; 3 = 32	
Linnet		
Distance to rape (c)	Median = 580 m; IQR = 737 m	Median = 581 m; IQR = 815 m
'Dgrass' adjacent (two levels)	1 = 227; 2 = 79	1 = 135; 2 = 71
'Ndgrass' adjacent (two levels)	1 = 217; 2 = 89	1 = 169; 2 = 37
Track (two levels)	1 = 224; 2 = 84	1 = 144; 2 = 62
Gullet rape (c)	Median = 0.740; IQR = 1.133	Median = 0.071; IQR = 1.124
Gullet dandelion (c)	Median = 0; IQR = 1.166	Median = 0; IQR = 1.124
Gullet *Stellaria* (c)	Median = 0.073; IQR = 0.291	Median = 0; IQR = 0.326
Gullet other (c)	Median = 0.045; IQR = 0.401	Median = 0.0; IQR = 0.464
Yellowhammer		
Habitat (two levels)	1 = 29; 2 = 183	1 = 14; 2 = 91
Maximum strip width (c)	Median = 2 m; IQR = 3 m	Median = 2 m; IQR = 4 m

c, 'continuous variable'; IQR, interquartile range.