Stabilizing selection on blue tit fledgling mass in the presence of sparrowhawks

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Like British great tits, Belgian blue tits have a lower winter body mass when sparrowhawks are present. Since body mass affects manoeuvrability in small birds, tits may balance the risks of starvation and the risk of hawk predation by varying the amount of extra fat carried during winter. Predation pressure by sparrowhawks on young and inexperienced fledglings is at least as intense as that on the adults during winter. We therefore expected that tit fledgling body mass could also be reduced in the presence of sparrowhawks. In the years after one pair of sparrowhawks settled in a study plot, the mean body mass of blue tit fledglings was lower compared with that in years when there were no sparrowhawks. Furthermore, the shape of the curve relating juvenile survival to fledgling mass changed, because the survival of the heaviest fledglings was reduced, which altered the selection differential of juvenile survival as a function of body mass from directional to stabilizing. Of seven published studies on the fledgling body mass–survival relation in tits, all three of the studies conducted in the absence of sparrowhawks showed the highest survival rates for the heaviest young, whereas in all four studies with sparrowhawks present this was no longer the case.

Keywords: *Accipiter nisus*; body mass; *Parus caeruleus*; predation; stabilizing selection; survival

1. INTRODUCTION

Small birds increase their fat reserves in winter as an insurance against reduced and unpredictable food supplies (Blem 1990). Since body mass affects flight manoeuvrability (Witter & Cuthill 1993; Witter *et al.* 1994), and heavier birds may suffer an increased predation risk by sparrowhawks, *Accipiter nisus* (Gosler *et al.* 1995; Witter & Cuthill 1993), less fat is carried when sparrowhawks are present (Gosler *et al.* 1995). Therefore, optimal winter body mass may be a variable compromise, balancing the risk of mortality through both predation and starvation (Gosler *et al.* 1995; Lima 1986; McNamara & Houston 1990).

According to textbooks (e.g. Gill 1995), it is generally true that 'a fledgling's chance of survival increases in proportion to its mass at fledging'. In the 1–2 weeks after fledging, sparrowhawks take up to 30% of young great tits, *Parus major* (Geer 1978, 1982; Perrins & Geer 1980; McCleery & Perrins 1991). Because body mass in fledglings should also affect flight manoeuvrability, one can expect that in the presence of hawks optimal fledgling mass could be lower than in their absence (Tinbergen & Boerlijst 1990).

Using the results from our long-term study of blue tits (*Parus caeruleus*) in Northern Belgium, we test the hypotheses that (1) as in British great tits winter body mass of Belgian blue tits is lower when sparrowhawks are present compared to when they are absent; (2) because the predation

pressure on fledglings is known to be very high, optimal fledgling body mass in blue tit fledglings is lower in the presence of sparrowhawks than when the sparrowhawks are absent; and (3) adult blue tits reduce their body mass when feeding nestlings in the presence of hawks more than when hawks are absent.

2. METHODS

The blue tit is a small songbird (mass *ca.* 11 g), closely related to the great tit. Both are common breeding birds in a wide variety of habitats. In Britain, as well as in Continental Europe, the sparrowhawk, one of its principal predators, was abundant until the late 1950s. But, especially in the 1960s and early 1970s, sparrowhawk numbers were severely reduced by organochlorine pesticide poisoning. Following regulation of the pesticides, population levels of sparrowhawks were restored rapidly during the 1970s and early 1980s (Newton 1986; Opdam *et al.* 1987; Gosler *et al.* 1995).

Between 1979 and 1993 we studied blue tit populations in two study sites in northern Belgium which contained a superabundance of nest boxes. Plot B was a study plot of 12.5 ha within a forest (over 400 ha). Plot C comprised an area of 17 ha in a private estate 2 km away from Plot B, and was separated from the larger forest by fields and houses (for more details see Dhondt 1987, 1989). In plot B, sparrowhawks were present all year round (throughout the study), sometimes breeding within the plot, sometimes in its immediate vicinity. In plot C, a sparrowhawk breeding pair first settled in 1990, and also during winter sparrowhawks were rarely seen before 1990 (Dhondt *et al.* 1998). No important changes to the habitat occurred in either plot during the study period. Because plot C is situated in a

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Table 1. *Effect of sparrowhawks on the body mass of blue tits in winter*

(Results of a mixed ANOVA with body mass as dependent variable and study area, period and the interaction as factors, and year nested within period YEAR(PERIOD) as random variable. The effect of the presence of sparrowhawks in Plot C is shown as a significant PLOT $\times$ PERIOD interaction, see §§ 2 and 3. Abbreviations: NDF, numerator degrees of freedom; DDF, denominator degrees of freedom.)

source	NDF	DDF	F	p
PLOT	1	1272	31.3	0.0001
PERIOD	1	15.3	1.16	0.2984
PLOT $\times$ PERIOD	1	1272	8.49	0.0036

private park containing many exotic trees and beeches, rather than in a forest of mainly mature oak trees (like plot B), breeding habitat quality is lower in plot C compared to plot B, resulting in an overall lower average fledgling body mass in plot C (Dhondt 1989). However, wintering conditions are probably better in parks than in forest (Dhondt *et al.* 1996).

Winter body mass of blue tits roosting in nest boxes was measured during the first hours after sunset between November and February. During the breeding season, adult birds were captured while feeding young of 8–10-days-old (before noon), and measured. Fledgling mass was measured at day 15, shortly before fledging. The presence of sparrowhawks during the breeding season caused an increase in the frequency of bigamy and single-parent broods through increased adult mortality (Dhondt *et al.* 1998). As these factors might have secondary effects on the body mass of the fledglings, we limited our analyses to monogamous, successful first broods (at least one fledgling) in which both parents were captured at the nest.

We used recovery rate of fledglings in the next breeding season as a measure of survival. All birds recovered during the breeding season were found by ourselves in one of our five study sites in the vicinity of plots B and C (C to C: $N=337$, B to B: $N=90$, C to others: $N=16$, B to others: $N=80$).

All analyses presented use the measured (i.e. unadjusted) values of body mass. Using the residuals of a regression of body mass against body size (tarsus) (and mean temperature on the day of capture for winter data; Gosler *et al.* 1995), resulted in qualitatively similar models (results not included).

To identify any influence of sparrowhawk presence, we compared individual traits between two study areas (PLOT) and two periods (PERIOD). In plot B, sparrowhawks were present throughout the study; in plot C they were present only in the period 1990–1993. In the pre-sparrowhawk (PRES P) period (1979–1989), no sparrowhawks were breeding in plot C; in the SP period, sparrowhawks were also breeding in plot C. We performed mixed ANOVAs (Littell *et al.* 1996), using plot B as a control. An effect of the presence of sparrowhawks in plot C is then shown as a significant PLOT $\times$ PERIOD interaction, representing a different effect of period in plot C and plot B. In all models, study area (PLOT), period (PERIOD), and the interaction (PLOT $\times$ PERIOD) were included. Year nested within period YEAR(PERIOD) was always entered as a random variable. Denominator degrees of freedom (DDF) were adapted for statistical dependence by Satterthwaite formulae (Littell *et al.* 1996).

Statistics were calculated using SAS v.6.12 (procedures GLM, MIXED and the GLIMMIX macro). Exact probabilities were calculated using StatXact v.3.0 (Mehta & Patel 1995).

Figure 1. (a) Mean fledgling mass, per year, in plot B (control area) and plot C (no sparrowhawks were present in the period 1979–1989, one pair bred in 1990–1993). (b) Difference in mean mass, per year, between plot B (control plot) and plot C. (The effect of sparrowhawks in the second period (to the right of the dotted line) is shown by the relative decrease in fledgling body mass in plot C).

3. RESULTS

(a) *Winter body mass*

Winter body mass of blue tits in plot C was lower in the SP period compared to the PRES P period, a change not observed in plot B. The significant PLOT $\times$ PERIOD interaction shows that these differences are statistically significant (table 1; parameter estimates ± 1 s.e.: plot B, 11.18 ± 0.08 to 11.18 ± 0.12 ; plot C, 11.60 ± 0.07 to 11.32 ± 0.11).

(b) *Fledgling body mass*

Mean body mass of blue tit fledglings in plot C was significantly lower in the SP period compared to the PRES P period, whereas there was no such change in plot B (figure 1). This resulted in a highly significant PLOT $\times$ PERIOD interaction in the mixed ANOVA, in which also NEST(PERIOD $\times$ YEAR) was entered as a random effect (see § 2, table 2; parameter estimate ± 1 s.e.: plot B, 11.16 ± 0.08 to 11.32 ± 0.11 ; plot C, 10.76 ± 0.08 to 10.38 ± 0.11).

The relationship between recovery rate and fledgling mass changed significantly between periods in plot C (see table 3 for the results of the logistic regression model). In the PRES P period, local survival increased monotonically with mass. In the SP period, local survival peaked at around 11 g, with heavier and lighter chicks having a

Table 2. *Effect of sparrowhawks on blue tit fledgling mass*

(Results of a mixed ANOVA, see §§2 and 3. Abbreviations: NDF, numerator degrees of freedom; DDF, denominator degrees of freedom.)

source	NDF	DDF	F	p
PLOT	1	840	178.9	0.0001
PERIOD	1	14.9	0.71	0.4130
PLOT × PERIOD	1	840	29.41	0.0001

Table 3. *Effect of the presence of sparrowhawks on the shape of the relationship between fledgling body mass and local survival in plot C*

(Results of a logistic regression model with local survival as dependent variable and period, mass, mass², and the interactions with period as factors, and YEAR(PERIOD) and NEST(YEAR × PERIOD) as random factors (see §§2 and 3). Abbreviations: NDF, numerator degrees of freedom; DDF, denominator degrees of freedom.)

source	NDF	DDF	F	p
PERIOD	1	5287	3.98	0.0460
MASS	1	5270	3.23	0.0723
MASS ²	1	5251	2.25	0.1339
PERIOD × MASS	1	5270	4.69	0.0303
PERIOD × MASS²	1	5251	5.27	0.0217

$$\text{SURVIVAL}_{\text{PRES}} = -4.59 - 0.51 \text{ MASS} + 0.053 \text{ MASS}^2$$

$$\text{SURVIVAL}_{\text{SP}} = -33.26 + 5.49 \text{ MASS} - 0.25 \text{ MASS}^2$$

lower local survival rate (figure 2). A similar analysis on the data for plot B resulted in non-significant factors only (all $p > 0.6$), showing no change in the form of the mass-survival relationship between the two periods. When study area and all interactions were entered in an analysis on the full data set, the model had to include a high number of intercorrelated factors. Nonetheless, the three-way interactions PERIOD × PLOT × MASS and PERIOD × PLOT × MASS² both showed, as predicted, that the effect of period was present in plot C yet absent in plot B (one-tailed test: $p = 0.053$ and $p = 0.039$, respectively). These changes between the PRES and the SP periods in plot C could not be explained by changes in breeding density (table 4), local survival (table 4) or the proportion of males (the heavier sex) among the locally recovered birds (PRES, 0.71, $N = 235$; SP, 0.74, $N = 89$; Fisher exact probability test, $p = 0.68$).

(c) *Adult body mass during the breeding season*

Although there were significant period effects on parental body mass, as well as on parental and nestling body size (tarsus length), none of the PLOT × PERIOD interactions were significant (table 4).

(d) *Adult breeding parameters*

To evaluate the effect of the presence of sparrowhawks on the breeding performance of the blue tit, we also analysed the effect on clutch size, fledging success (number of fledglings per egg) and number of fledglings (table 4). In the presence of sparrowhawks, blue tits tend to lay comparatively fewer eggs (PLOT × PERIOD inter-

Figure 2. Local recovery rate of blue tit fledglings in the next breeding season as a function of fledgling body mass in plot C. Symbols: proportion of surviving birds per 0.5 g mass classes (at least three recoveries per class). Lines: results of a logistic regression model (see table 3, §3).

action $p = 0.06$, parameter estimate ± 1 s.e.: plot B, 11.19 ± 0.21 to 10.85 ± 0.25 ; plot C, 11.63 ± 0.24 to 10.77 ± 0.24). However, fledging success is relatively higher (parameter estimate ± 1 s.e.: plot B, 0.86 ± 0.01 to 0.80 ± 0.02 ; plot C, 0.84 ± 0.01 to 0.85 ± 0.02), and the effect on the resulting average number of fledglings is not significant (parameter estimate ± 1 s.e.: plot B, 9.70 ± 0.18 to 8.77 ± 0.30 ; plot C, 9.75 ± 0.17 to 9.12 ± 0.29).

4. DISCUSSION

(a) *Adult winter body mass*

In the presence of sparrowhawks, blue tit winter adult body mass in plot C was relatively lower compared to the control area, as predicted from Gosler *et al.*'s (1995) results for British great tits. Great tits (Gosler 1996) and European starlings (*Sturnus vulgaris*; Witter & Swaddle 1995; Witter *et al.* 1995) can and do actively regulate fat reserves during winter in relation to day temperature, day length, food predictability, dominance status and competition. Caged greenfinches, *Carduelis chloris*, with unlimited access to food suffered lowered body masses when a stuffed hawk was shown to them five times a day (Lilliendahl 1997). The observation that, during winter, birds in the field actively regulate their body mass, and that caged birds (Lilliendahl 1997) or free-living birds (Gosler *et al.* 1995; this study) carry less fat or weigh less during winter in the presence of hawks, strongly suggests that these changes represent adaptive regulation. Our results on winter body mass also confirm Gosler *et al.*'s (1995) conclusion that the change is mainly phenotypic, because body size did not change in parallel to body mass.

(b) *Adult body mass in the breeding season*

During the breeding season also, there is some evidence that at certain points in the breeding cycle female blue tits actively regulate their body reserves to optimize their

Table 4. *Effect of sparrowhawks on parental body size (tarsus) and breeding season mass, fledgling body size, breeding density and local survival*

(Results of mixed ANOVAs, see §§ 2 and 3. Abbreviations: NDF, numerator degrees of freedom; DDF, denominator degrees of freedom.)

dependent variable	source	NDF	DDF	<i>F</i>	<i>p</i>
tarsus parents	PLOT	1	1321	7.67	0.0057
	PERIOD	1	12.9	7.98	0.0144
	PLOT × PERIOD	1	6321	0.61	0.4348
mass parents	PLOT	1	1340	29.2	0.0001
	PERIOD	1	15.1	5.33	0.0355
	PLOT × PERIOD	1	1340	1.25	0.2633
tarsus fledglings	PLOT	1	806	0.33	0.5662
	PERIOD	1	13.9	12.0	0.0039
	PLOT × PERIOD	1	806	0.09	0.7697
breeding density	PLOT	1	12	0.48	0.5026
	PERIOD	1	12	0.00	0.9941
	PLOT × PERIOD	1	12	0.04	0.8493
local survival	PLOT	1	1203	6.58	0.0104
	PERIOD	1	14.29	0.14	0.7110
	PLOT × PERIOD	1	1203	1.56	0.2117
clutch size	PLOT	1	796	1.70	0.1928
	PERIOD	1	13.5	8.76	0.0107
	PLOT × PERIOD	1	796	3.51	0.0614
number of fledglings	PLOT	1	795	1.06	0.3040
	PERIOD	1	14.6	7.61	0.0149
	PLOT × PERIOD	1	795	0.57	0.4506
fledgling success	PLOT	1	785	0.49	0.4836
	PERIOD	1	15	2.34	0.1471
	PLOT × PERIOD	1	785	4.64	0.0316

breeding performance (Woodburn & Perrins 1997). Nevertheless, we did not find an effect of sparrowhawk presence on parental body mass during the nestling stage. The blue tits' body reserves are probably very low already, because of high energetic stress and/or adaptive processes to reduce flight costs (Woodburn & Perrins 1997, and references therein), so that adults only carry minimal fat reserves anyway, and hence cannot reduce body mass any further in the presence of sparrowhawks.

(c) *Fledgling body mass*

After sparrowhawks settled in plot C, fledgling body mass became relatively lower compared to that in the control plot, as shown by the highly significant Plot × Period interaction (table 2). However, this did not coincide with a change in nestling tarsus length, a heritable measure of body size (Dhondt 1982) (no significant Plot × Period interaction, cf. table 4). The shape of the curve describing juvenile survival as a function of fledgling mass also changed in plot C: in the PRESP period, it was a monotonically increasing relationship; in the SP period it became a curve with an optimum of around 11 g (figure 2). In plot B, where sparrowhawks had been present throughout the study, there existed no significant relationship between body mass and fledgling survival in either

period. Specifically, survival of the highest mass class was not higher than survival in some of the lower classes, nor did survival differ between the two periods.

(d) *Is the result an artefact?*

We first need to consider if the observed reduction in survival rate of the heaviest chicks in plot C could be an artefact, caused by increased dispersal of heavier juveniles in the presence of sparrowhawks. Body mass of nestlings was not related to dispersal tendencies. Because no birds were recovered breeding outside plot C in the SP period, we can only show that in the PRESP period dispersal was not related to body mass in either plot. An ANOVA with Status and Plot and the Status × Plot interaction showed a significant effect for plot only ($F_{1,405}=9.49$, $p=0.002$; plot B, 11.35 ± 0.06 , plot C, 11.05 ± 0.05). Neither dispersal status ($F_{1,405}=0.03$, $p=0.86$; local, 11.04 ± 0.05 ; dispersed, 11.07 ± 0.1) nor PLOT × STATUS interaction ($F_{1,405}=1.14$, $p=0.29$) were statistically significant. Similarly, in Swedish studies on blue tits, no differences in nestling mass or size were found with dispersal distance (Dhondt 1979; Smith *et al.* 1989), or between blue tits recaptured during migration as compared to those that were recovered locally during winter (Smith & Nilsson 1987).

If dispersal increased in the SP period compared to the PRESP period, the number of juveniles born in plot C that were recovered in plot B should be higher in the SP period than in the PRESP period. This was clearly not the case. Similarly, we would expect an overall decrease in local recovery rate in the SP period. This was not the case: the local recovery rate in the PRESP period was 3.3%, compared with 3.9% in the SP period. We believe, therefore, that the change in the relationship between fledgling mass and survival between the PRESP period and the SP period is not the result of more of the heavier birds dispersing in the SP period, and reflects a change in survival, not in dispersal.

(e) Is the result repeatable?

We know of seven published studies that permit verification of our result that in tits (great and blue tits combined) the shape of the relationship between mass and survival depends on the presence of sparrowhawks. In all three studies from the 1950s and 1960s, when sparrowhawks were very rare throughout north-western Europe (see §2), the heaviest chicks survived best (Dhondt 1971; Garnett 1981; Perrins 1965). In all four studies carried out after 1975, when sparrowhawks had become re-established, this was no longer found to be the case: heavier chicks did not have the highest survival rates. Survival either did not change with fledgling mass, or the survival rate peaked at an intermediate value (Julliard *et al.* 1996; Lindén *et al.* 1992; Nur 1984; Tinbergen & Boerlijst 1990). This result is not expected by chance (Fisher exact probability test, $p=0.029$). In Wytham Woods (Oxfordshire, UK), as in plot C, the shape of the mass-survival relationship changed according to the presence or absence of sparrowhawks (Garnett 1981; Nur 1984; Perrins 1965). It seems likely, therefore, that the large variation in the shape of the curves relating fledgling body mass to survival within one species, indeed, within the same population, may be due to changes in the presence/absence of sparrowhawks at the time of data collection.

(f) Is the change adaptive?

In the presence of sparrowhawks in plot C, heavier fledglings were selected against and mean fledgling mass was reduced, meaning that optimal fledgling mass had decreased. It is very difficult to decide if we should consider this change to be an adaptive one, or whether it simply results from a constraint. If it is an adaptive one, is the reduced fledgling mass the result of a decision of the nestlings or of the parents? Asymmetries in cost and benefits between parents and offspring also come into play.

As the matter stands, our data do not allow us to draw any definite conclusions in respect to the actual mechanism involved. It seems unlikely that chicks of cavity-nesting species would beg less in the presence of sparrowhawks, or that parents would actively decide to provide less food while the chicks are begging at the same rate. However, a recent study by Leech & Leonard (1997) does show that predation risk may be increased by begging calls in artificial nests, even in cavity-nesters. In our study, clutch size tended to be lower in the presence of the hawks, but not nest success or the final number of fledglings. This result could be interpreted as indicating that adults are

anticipating food-provisioning problems while feeding the chicks, and thus as some form of adaptive response, balancing the cost of predation risk.

It is generally accepted that adult or territory quality is directly translated into fledgling survival, via fledgling mass, and that fledgling mass is therefore a good estimator of fitness (Gill 1995; Tinbergen & Boerlijst 1990). However, our data show that this relation should be treated with great care. As is true for adults (Gosler *et al.* 1995; Lima 1986), predation might limit the survival value of high fledgling body mass in any species, changing the selection differential from directional to stabilizing (see also Lindén *et al.* 1992). In the presence of avian predators, the optimal body mass, even of fledglings, could be well below the maximum observed.

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