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Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*

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The optimal amount of reserves that a small bird should carry depends upon a number of factors, including the availability of food and environmental predation risk levels. Theory predicts that, if predation risk increases, then a bird should maintain a lower level of reserves. Previous experiments have given mixed results: some have shown reduced reserves and some, increased reserves. However, the birds in these studies may have been interpreting a staged predation event as a period when they were unable to feed rather than a change in predation risk: theory predicts that, if the food supply within the environment is variable, then reserves should be increased. In the present study, we presented blue tits (*Parus caeruleus*) with a potential predator and compared this response (which could have been potentially confounded by perceived interruption effects) with a response to an actual interruption in the environment during both long and short daytime lengths. During long (but not short) days, the birds responded in line with theoretical predictions by increasing their reserves in response to interruption and reducing them in response to predation. These results are examined in the light of other experimental manipulations and we discuss how well experimental tests have tested the predictions made by theoretical models.

Keywords: predation risk; foraging; mass regulation; *Parus caeruleus*; interruption

1. INTRODUCTION

Predation risk has been argued to be one of the key ecological factors determining the body mass of birds (Lima 1986; McNamara & Houston 1990; Houston *et al*. 1993; Rogers & Smith 1993; Witter & Cuthill 1993; McNamara *et al*. 1994; Cuthill & Houston 1997; Houston *et al*. 1997). Maintaining a high body mass is predicted to increase the risk of predation due to both increased amounts of foraging time necessary for keeping reserve levels high and impairment of manoeuvrability during escape from the predator. The latter is due to mass-dependent effects on flight performance: increasing body loads has been shown to have an effect on aspects of take-off ability in some species (Jones 1986; Metcalfe & Ure 1995; Kullberg *et al*. 1996; Lee *et al*. 1996; Lind *et al*. 1999; but see Kullberg 1998; Kullberg *et al*. 1998; Veasey *et al*. 1998; Van der Veen & Lindström 2000). Theoretical models (Lima 1986; McNamara & Houston 1990; Houston & McNamara 1993; McNamara *et al*. 1994) have predicted that, if predation risk is mass-dependent, an increase in risk should lead to a decrease in the level of reserves that the bird carries.

Witter *et al*. (1994) investigated the effects of perceived predation risk by manipulating the amount of protective cover available to starlings and demonstrated that their fat scores were positively related to cover availability, although their actual wing loadings appeared unaffected. A reduction in body mass in response to the simulated presence of a predator has been seen in greenfinches (*Carduelis chloris*) (Lilliendahl 1997, 2000), coal tits (*Parus ater*) (Carrascal & Polo 1999) and yellowhammers (*Emberiza citrinella*) (Van der Veen 1999*a*,*b*; Van der Veen & Sivars 2000). However, other experiments have shown that yellowhammers (Lilliendahl 1998), migrant blackcaps (*Sylvia atricapilla*) (Fransson & Weber 1997) and tufted titmice (*Baelophus bicolour*) (Pravosudov & Grubb 1998) increased their mean mass in response to increased predation risk. Coal tits have also been shown to increase their evening mass in response to increased nocturnal predation risk (discussed in Bautista & Lane 2000).

Theory (McNamara & Houston 1990; Houston & McNamara 1993; Bednekoff & Houston 1994; McNamara *et al*. 1994) predicts that the energetic environment is also important in determining the optimal levels of reserves that birds carry. Increasing the variance of gain or the chance of foraging being interrupted should lead to an increase in optimal reserve levels. This has been demonstrated experimentally in various species (Ekman & Hake 1990; Bednekoff & Krebs 1995; Witter *et al*. 1995; Witter & Swaddle 1997; Cuthill *et al*. 2000; but see Dall & Witter 1998), although all but one of these experimental studies failed to separate the effects of being interrupted from changes in the variability and predictability of the food supply (Cuthill *et al*. 2000), which limits the conclusions that we can draw from them. Several authors (Lilliendahl 1998; Pravosudov & Grubb 1998; Carrascal & Polo 1999; Van der Veen & Sivars 2000) have suggested that, in studies of perceived predation risk where 'predated' birds have increased in mass, these birds may have been responding to the predation event as if it were an interruption in the food supply. With the exception of Van der Veen & Sivars (2000), few studies have attempted to separate the effects of a predation attempt in terms of a

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perceived increase in predation risk or as an interruption to foraging. The study by Carrascal & Polo (1999) attempted to do so, but predation and interruption were investigated in two separate experiments using different timing regimes, which confounds the conclusions that we can draw. The experiment we describe attempts to disentangle these effects by subjecting birds to perceived 'predation' events and periods where the food supply was removed for an identical period of time.

2. METHODS

We used 13 one-year-old female blue tits (*Parus caeruleus*) that had been mist netted under English Nature licence: ten (one replacing a bird that died during the summer phase of the experiment) were caught between late January and early March 1998 at the University of Bristol Botanic Gardens in Leigh Woods, North Somerset, UK and three were caught in Surrey, UK, in mid-February 1998. Seven of the Bristol birds were used in the 'long day' phase of the experiment and the rest were used in the 'short day' phase. All birds were sexed by R. Griffiths (Griffiths *et al*. 1998) and had been used previously for the (unrelated) experiments described by Hunt *et al*. (1998, 1999). After capture, the birds were kept in individual cages in an indoor aviary with a daylight-mimicking light source (UV rich) set at natural light:dark cycles. For this experiment, the birds were moved to individual, adjacent covered outdoor aviaries on the roof of the University of Bristol School of Biological Sciences (2° 36′ W 51° 27′ N) and experienced at least three days in the roof aviary prior to any data being recorded from them. Each aviary had an entry door and a shelf accessible from outside the cage via a maintenance hatch. A waterproofed 32.5 cm × 20 cm × 9 cm plywood box, which was designed to hold an Ohaus E400 electronic balance, was placed on each of these shelves. A 17.5 cm × 20 cm hole was cut in the top of the box and covered with a black plastic sheet, so that a food bowl could be placed on top of the (covered) balance. A water bowl was also placed on the box. If the box did not contain one of the two balances used, then the plastic sheet was held in place by placing a cardboard stand inside the box. The birds were left undisturbed by human presence except for periods when manipulation occurred and also when food and water were replenished (from outside, via the hatch). During these periods all the birds were briefly inspected and any vital maintenance was carried out.

The experiment ran from 6 to 20 June and 2 to 14 July (the long day period) and 27 October to 20 November (the short day period) 1998. The birds were supplied with an *ad libitum* mixture of Orlux Universal Softbill food, dehusked sunflower seeds, crushed peanuts, grit and mealworms throughout the experiment. During the experiment, the food supply was replenished and the water supply replaced each day between 21.00 and 03.00 h Greenwich Mean Time, when the balance output was not being recorded and the birds were at roost. During this period, the balances and card stands were removed and repositioned in all the cages and the balances were recalibrated.

The output from the balances was recorded on experimental days between 03.00 and 21.00 h. The masses (to 0.01 g) of the food bowls in the treatment cages were monitored using the 'Nestbug' package (Szép *et al*. 1995), run in MS-DOS on a Viglen PC. The program was used for calculating the mass and timing of a bird landing on and departing from the food bowl.

Each bird underwent each of the four different treatments once. The order and timing of each bird's treatments were randomly allocated within a yoked, balanced design. Experimental treatments occurred in pairs of pairs. On the first day of each quartet, the experimental bird experienced a predation event, whilst a control bird experienced no predation. On the second day, an experimental bird experienced an interruption event, whilst a second control bird experienced no interruption. Both events for each pair within the quartet occurred either in the morning (at 08.00 h) or in the afternoon (at 16.00 h). Whether an event was in the afternoon or morning was randomly allocated following a balanced design. During a predation event, S. A. Rands entered the cage of the experimental bird wearing a laboratory coat, pursued the bird for 60 s with one hand and then promptly exited the cage. The time taken between the start of the predation event and the bird next landing on the food bowl was calculated. Control birds were not chased on predation days, but were able to hear alarm calls from the chased birds.

On the second day of a treatment pair an interruption treatment was carried out, which was designed so that feeding was prevented for an identical duration to that experienced by the experimental bird on the previous day. The experimental bird's food bowl was removed for the period calculated for the previous day, but the cage was not entered and the bird was not chased. The food bowl was removed via the maintenance hatch and replaced with an identical but empty bowl during the removal time. Any food scattered around the bowls was also quickly removed whilst carrying out the manipulations. On interruption days, the corresponding control bird had its food bowl and any scattered food removed, but the bowl was replaced immediately after it had been withdrawn from the cage. On two afternoon treatment days of the short day experiment, birds that were 'predated' did not return to the feeder before the end of the day. In these cases, an estimated interruption time was calculated by taking the mean of all the short day afternoon interruption lengths that had already been recorded.

The birds were monitored throughout the experiment and appeared not to show any adverse reactions to the manipulations. Chasing has previously been shown to have effects on allocation decisions in coal tits, where the birds were chased for 6 min four times a day (Carrascal & Polo 1999). Blue tits are broad-leaf deciduous woodland birds (Perrins 1979) and spend most of their time foraging in or close to trees. When they encounter predators, they will typically flee immediately to shelter, where they will remain motionless for a period of time (Hegner 1985). Although the aviaries did offer some shelter in the more inaccessible corners of the cages, the tits were relentlessly pursued during the predation treatment without allowing them the opportunity of hiding or resting. We judged 1 min of chasing to be suitable as this was near the upper limit of the time it can take to catch a blue tit in the cages by pursuing them with a butterfly net during routine inspections (S. A. Rands, personal observation). For this reason, whilst the bird is stressed, the severity is no greater than that which can be experienced as a part of normal husbandry (e.g. capture for veterinary inspection). After the experiments, most birds were retained in the roof aviaries until the weather conditions were suitable for release in the location of their capture (within six months) (see the ethical note in Hunt *et al*. (1999) for details of the release method). A number of birds were humanely killed for histological measurements that were unrelated to the present experiment.

Table 1. Results of repeated-measures ANOVAs testing for differences in the mean mass change between the hour before and after a perceived predation event, the number of visits to the feeder in the hour after the target-predated bird had first returned and the mass change between the pre- and post-treatment phases of the day.

(Only the results for the main effects (which were nested in the model used) are given. None of the interaction terms approached significance (in all cases, $F_{1,5} < 3.47$ and $p > 0.120$, except for the short day differences in mass change where $F_{1,3} < 0.63$ and $p > 0.485$). Levels of significance: $^{*}p < 0.05$ and $^{\text{n.s.}}p > 0.05$.)

	mean mass change		feeding activity change		rate of mass change
phase of experiment	long day	short day	long day	short day	for a long day
control versus treatment	$F_{1,5} = 19.209$ and $p = 0.007^{*}$	$F_{1,3} = 0.284$ and $p = 0.631^{\text{n.s.}}$	$F_{1,5} = 2.436$ and $p = 0.179^{\text{n.s.}}$	$F_{1,5} = 1.145$ and $p = 0.334^{\text{n.s.}}$	$F_{1,5} = 0.010$ and $p = 0.925^{\text{n.s.}}$
time of day	$F_{1,5} = 0.021$ and $p = 0.890^{\text{n.s.}}$	$F_{1,3} = 0.011$ and $p = 0.923^{\text{n.s.}}$	$F_{1,5} = 0.052$ and $p = 0.829^{\text{n.s.}}$	$F_{1,5} = 13.878$ and $p = 0.014^{*}$	$F_{1,5} = 4.476$ and $p = 0.088^{\text{n.s.}}$
predation versus interruption	$F_{1,5} = 8.102$ and $p = 0.036^{*}$	$F_{1,3} = 0.597$ and $p = 0.496^{\text{n.s.}}$	$F_{1,5} = 1.192$ and $p = 0.325^{\text{n.s.}}$	$F_{1,5} = 1.814$ and $p = 0.236^{\text{n.s.}}$	$F_{1,5} = 1.166$ and $p = 0.330^{\text{n.s.}}$
before versus after treatment	—	—	—	—	$F_{1,5} = 11.683$ and $p = 0.019^{*}$

3. STATISTICAL ANALYSIS

The data were examined for background noise (due to the effects of wind and the weather upon the equipment) and records that could not be attributed to a bird landing on the feeding bowl were removed. These were taken to be values less than 8 g or greater than 15 g (the mean first mass measured during a day was 10.04 ± 0.94 g (s.d.) and the mean final mass was 10.91 ± 1.12 g, both of which were calculated from 96 observations across all individuals). In order to examine the direct effects of the manipulation, we calculated the mean arrival mass of each bird during the hour before the experimental manipulation (or the corresponding period for the control birds) and the mean arrival mass during the hour after the target-'predated' bird had returned to the feeder. For the long day treatment, we calculated the rate of mass change before and after the treatment by conducting least-squares linear regressions upon the complete datasets of masses from before a target treatment began and after a target treatment had ended (there were insufficient data for calculating these for the short day experiment). The number of visits to the feeder during the hour after the target bird had returned was also calculated as a measure of the activity of an individual in direct response to the treatments.

Because each bird was subjected to all the experimental manipulations, we conducted a number of repeated-measures analyses of variance (all residuals were normally distributed) with SPSS 8.0, using 'day type' (whether the bird experienced a predation day or an interruption day), 'control' (whether the bird was an experimental or a control individual) and 'time of day' (whether the treatment occurred in the morning or afternoon) as within-subject factors in the design. Therefore, each bird experienced eight treatments: two experimental treatments and two control treatments, each at two times of day. Due to the nesting of treatments, the maximum sample size was six birds. However, due to some of the birds not visiting the feeding sites in the early or late periods of the days, the corresponding sample sizes of these periods were reduced. The equipment malfunctioned on three days during the long day treatment, resulting in three of the six samples having a single treatment and a single control value missing. As none of these occurred with the similar within-subject factor nestings, we estimated the values for the treatment and control by taking the mean of the other three records for the treatment or its controls under the assumption that using a mean value would make it more difficult to detect a significant difference between the means calculated in the ANOVA, thereby increasing the likelihood of a type II error. The effect of the manipulations upon the start and end times of activity was tested using a Friedman analysis of variance as the assumption that residuals were normally distributed was violated.

Ekman & Hake (1990) noted that greenfinch reserves fell during the first few weeks of captivity and then levelled off. This suggests one criticism that might be levelled at our experiment in that, although the birds had been in captivity for at least two months in internal aviaries before the experimental manipulations were carried out, some of the birds were only moved to the roof aviaries a few days before the experiment. The pairing of both daily treatment types and control and treatment birds should have minimized the effects of any continuing changes in response that were due to being moved outside, and the entire design was balanced for date of manipulation.

4. RESULTS

When testing for the effects of the various manipulations upon the change in mean mass between 1 h before and 1 h after the treatment, control and treatment birds differed significantly in their response during the long day phase of the experiment (table 1): treatment birds tended to gain mass, whilst control birds lost mass (figure 1*a*). There was no significant difference in response to the morning or afternoon predation events. Predated and interrupted birds (and their controls) differed significantly in their response to the manipulation: birds measured on predation days tended to lose mass, whereas birds measured on interruption days increased their mass. When examining the responses of treatment and control birds during either predation or interruption, the control birds lost a greater amount of mass than the treatment birds for both treatment types, with the greatest amount of loss occurring on predation days. During the short day phase

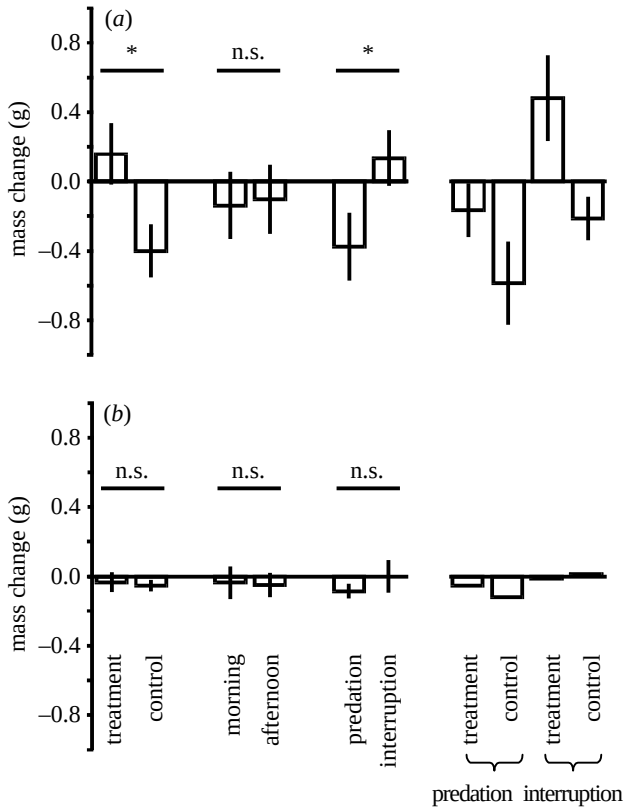

Figure 1. Mean mass changes (±s.e.) between the hour before the treatment and the hour after the target bird returned in (*a*) the long day phase and (*b*) the short day phase of the experiment for the estimated means of the various treatment types conducted (adjusted means calculated using SPSS 8.0). The means when considering the (non-significant) interactions between treatment type and control type are also shown. Levels of significance: $^{*}p < 0.05$ and $^{n.s.}p > 0.05$.

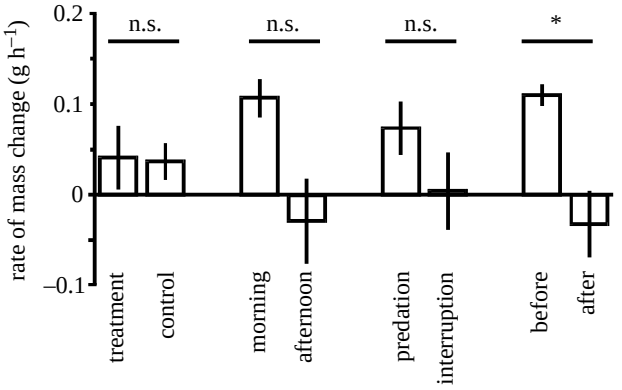

Figure 2. Estimated marginal mean rates of mass change (±s.e.) in the periods before and after a treatment during the long day experiment for the various treatment types conducted. Levels of significance: $^{*}p < 0.05$ and $^{n.s.}p > 0.05$.

of the experiment, there were no significant effects of any of the treatment factors upon the mass changes shown by the birds (table 1 and figure 1*b*). Predated birds stayed away from the feeder for 42.50 ± 36.82 min (s.d.) ($n = 12$) during the long day phase of the experiment and 21.52 ± 8.50 min ($n = 10$) during the short day phase.

Table 1 gives the results of the ANOVA testing for effects upon the feeding activity of individuals in response to the various treatments, which was measured as the number of visits made to the feeder in the hour after the target bird initially returned to the feeder. The long day experiment showed no significant differences in the responses of individuals (estimated marginal mean number of visits (±s.e.), morning 7.4 ± 0.8, afternoon 7.1 ± 2.3, predation 5.7 ± 0.3, interruption 8.8 ± 3.0, control 6.2 ± 1.1 and treatment 8.4 ± 2.1), whereas the numbers of visits made after a morning treatment (17.8 ± 3.9) were significantly greater than after an afternoon treatment (2.0 ± 0.8) during the short day experiment, whilst the other responses did not significantly differ (predation 8.6 ± 1.8, interruption 11.1 ± 2.4, control 8.3 ± 1.0 and treatment 11.5 ± 3.3).

The rates of mass change differed significantly between pre-and post-treatment birds (table 1), with pre-treatment birds tending to gain mass, whilst post-treatment birds tended to lose mass (figure 2). Although not significant, there was also a tendency for birds to gain mass over the course of days in which a treatment occurred in the morning and to lose mass on days with afternoon treatments.

As to be expected, there were no effects of treatment upon the timing of the start of daily activity (Friedman ANOVA, long days $\chi^2_7 = 3.44$ and $p = 0.841$ and short days $\chi^2_7 = 8.28$ and $p = 0.309$) and there were no effects upon the timing of the end of activity (long days $\chi^2_7 = 6.67$ and $p = 0.464$ and short days $\chi^2_7 = 8.39$ and $p = 0.300$), suggesting that there were no effects of treatment upon the length of a bird's daily routine.

5. DISCUSSION

This experiment demonstrated that, during long days, blue tits show markedly different short-term mass changes in response to a change in perceived predation risk and to an interruption of the food supply within the environment. Taken at face value, these responses agree with theoretical predictions: mass is reduced in response to increased predation risk and is increased in response to an increasingly unpredictable environment (McNamara *et al*. 1994), as illustrated in figure 3*a*. Our analysis compared the mean mass over 1 h before and 1 h after the treatment rather than the exact masses immediately pre- and post-treatment, as in Van der Veen & Sivars (2000), which would have been difficult to estimate due to background noise caused by wind. Because we considered averages, this did not allow us to ascertain the exact mechanism behind the differing responses to the treatments. It is likely that the treatment birds lost mass during the treatment period as they did not have access to food and so they should have been regaining this lost mass during the post-treatment period, as in Lilliendahl (2000) and Van der Veen & Sivars (2000).

Several mechanisms could explain the patterns of mass change observed, as outlined in figure 3. Individuals could have lost mass at the same rate during either treatment type and differed in their post-treatment responses (figure 3*b*), either through physiological differences in their efficiency of nutrient assimilation or through behavioural differences in the amount of food taken per visit

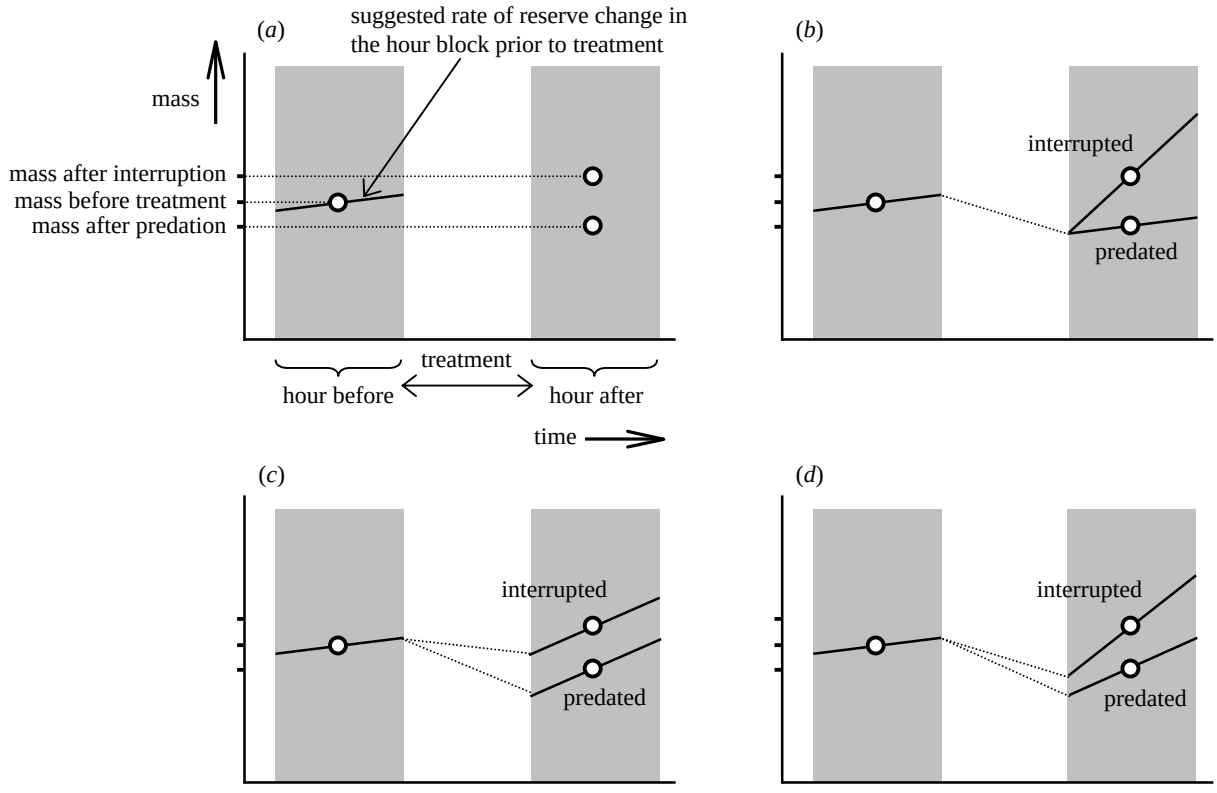

Figure 3. (*a*) Patterns of mass change seen in response to interruption and predation and possible mechanisms explaining these patterns: (*b*) differences occurring post-treatment, (*c*) differences occurring during the treatment and (*d*) differences occurring during both periods.

to the feeder, the rate of visiting and changes in the amount of energetically expensive activities conducted. Alternatively, if both the interrupted and predated birds had fed and assimilated food at the same post-treatment rate, this would suggest that the predated birds lost more mass during the treatment period (figure 3*c*), which could again be through changes in physiological processes or differences in activity (the predated birds did experience 1 min of escape flight when being chased) or through predated birds losing excess mass through defecation (Van der Veen & Sivars 2000). Finally, a combination of both these mechanisms could have been occurring (figure 3*d*). The evidence from comparing the activity rates in this study suggested that differences in loss were not due to changes in post-treatment feeding behaviour: the only significant difference in activity (number of post-treatment visits to the feeder) in response to the treatments occurred in the short day experiment when morning birds visited more than afternoon birds, but this can be attributed to the normal pre-dusk foraging activity of the birds rather than a response to the experimental manipulations (which had no significant effects). The study by Van der Veen & Sivars (2000) showed significant differences between the immediate mass changes of yellowhammers in response to interruption and to combined predation and interruption, suggesting that the differences in the rate of loss during the treatment period was the more likely explanation. In our study, differences did occur in the rate of mass change before and after treatment, but this appeared to be related to time of day rather than predation risk. The post-treatment rates of change tended to show a slight decrease in mass, which may have been due to end-of-day effects: the tits may have ensured that their reserves were sufficient for surviving the night and, thus, were able to mobilize some of their stored reserves in the latter part of the day. Different mechanisms may have been in operation immediately following the treatment, but our data were insufficient for testing this. In order to elucidate the mechanism in blue tits, we need to conduct experiments that allow us to examine the immediate post-treatment response to a finer degree than was possible with the experiment described here.

In addition to an effect upon the levels of reserves in response to changes in the environment, the models of McNamara *et al*. (1994) and Bednekoff & Houston (1994) (considering pre-migratory birds) also predicted that there would be a change in the timing of allocation decisions during the day. With an increase in predation risk, birds will not only have lowered levels of resources during the day, but will also postpone most of their foraging (the high predation risk activity) until the last few periods of the day, with associated increases in reserves. This effect has been demonstrated experimentally in yellowhammers (Van der Veen & Sivars 2000). The blue tits in this study did not show any obvious patterns of change in their behavioural routines or mass allocation during the course of the day (between morning and afternoon treatments). This could have been because the birds in this experiment were constrained by the degree

of response they were able to give to the treatments. This study tested predictions generated by stochastic dynamic programming (Mangel & Clark 1988; Houston & McNamara 1999), which are normally presented as the average response of a population. Because of this averaging, the actual response of one individual may differ greatly from that of another and should ideally be tested for by mixing simulation with repeated measurement and testing of an individual's response (Hutchinson & McNamara 2000).

We must also ask whether the experimental animals perceived the effects of the manipulation in the desired manner. The response of individuals may depend upon whether they perceive a change in the environment to be short-term or long-term (see, for example McNamara & Houston 1994) and whether the manipulation is causing a change in behaviour due to a change in policy at a given state or due to a manipulation of an individual's state with no change in policy (Hutchinson & McNamara 2000). Most of the predation risk studies that have been carried out (including this one) may not have directly manipulated birds' perceptions of the environmental predation risk and, hence, changed their optimal policy. Instead, the birds were faced with a direct predation event, which would have changed their state (energetic reserves and/or immediate predation risk) but not necessarily their optimal policy based on long-term environmental conditions. A surprising result from this study was that the control birds tended to show mass loss during the long day treatments. From theory, control birds should show less mass gain than treatment birds following an interruption, and the pattern seen here was consistent with this (figure 3*a*). However, the control birds tended to lose more mass than treated birds on predation days, a trend that requires explanation. Due to the aviaries being adjacent, all of the birds would have been able to hear the alarm calls of the pursued bird and may have been able to see an obscured view of the 'predator' during the treatment. It may be that experiencing a predation attempt (and being chased) had a very different effect upon an individual's routine when compared with gaining information about the presence of something in the environment that causes a close neighbour to give repeated alarm calls (see also Van der Veen 1999*b*). Hearing alarm calls is likely to be interpreted as an increase in predation risk, but, unlike the chased bird that 'escapes' the predator when the latter leaves the aviary, the control bird has no direct information that the predator has departed. Therefore, contrary to the design of the experiment, the control bird might experience a longer period of elevated predation risk than the chased bird. This hypothesis could be tested by examining the responses of individuals to recorded alarm calls, where the arrival and departure of the predator is or is not clearly signalled. A similar response to that observed here, when predator departure is uncertain, would suggest that information from neighbours is integrated with direct personal experience when an individual makes decisions about its routine. Another possible effect upon perceived predation risks could have been through human presence during the routine maintenance of the birds (which was conducted at night in order to minimize interruption), although the experiment was designed so that any maintenance (and, hence, potential predation risk) effects were experienced equally by all the birds (regardless of whether they were being experimented upon during the previous or following days).

Another way around the problem of knowing what effects a manipulation has upon birds' perceptions of their environment would be to measure the changes in the daily routines of birds that are subjected to a regime where risk is manipulated through the continuous appearance of a predator. Van der Veen (1999*b*) showed that the schedules of yellowhammers changed in response to the repeated appearance of a model predator over several days. Therefore, investigating only the immediate response of a bird to the presence of a predator may not reveal the longer-term response of the individual to changes in its environment.

Comparison between the results of this and other studies is confused by different studies using birds at different stages of their annual cycle, as some birds were tested mid-migration (e.g. Fransson & Weber 1997) and others during their wintering period (e.g. Lilliendahl 1997): this may have great effects on their priorities in the allocation of their time and resources. This experiment suggested that differences can exist within a species at differing times of year. The blue tits apparently responded as predicted by theory during the long day phase, but failed to show any significant patterns of response to the short day phase. This could be because the shortened daylight foraging period meant that the birds had to forage constantly in order to maintain reserves, thereby reducing the impact that predation risk has upon their behavioural policies. If reserves are so important when days are short, it could be asked why birds experiencing interruption do not increase their foraging rates after being unable to access food for a period of time. It may be that the birds are already working at the upper limits of their energetic expenditure (Hammond & Diamond 1997) and are unable to increase their efforts to compensate for the lack of food collected during the interruption period.

Although we have demonstrated here that blue tits can respond to predation and interruption with the responses predicted, the fact that some previous studies (Fransson & Weber 1997; Lilliendahl 1998; Pravosudov & Grubb 1998) have not demonstrated these responses does not necessarily mean that the birds in these studies were responding to the predation treatment as an interruption rather than a predator. All the studies conducted to date have used very different methods for testing predation risk (see Carrascal & Polo 1999). Many authors (Metcalfe & Ure 1995; Kullberg *et al*. 1996; Fransson & Weber 1997; Lilliendahl 1998; Pravosudov & Grubb 1998; Carrascal & Polo 1999; Van der Veen & Lindström 2000) have suggested that the difference between the habitats of the test species and their responses to predators could have a large effect upon their patterns of response to experimental predation. However, comparison is impossible at present due to the great differences in experimental design and the problems of most manipulations failing to disentangle predation and interruption. The study described here suggests that it is possible to separate these effects experimentally and, hence, we may eventually be

both able to test theoretical predictions satisfactorily and compare the responses of species with different life histories and ecologies.

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