Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*

R. MACLEOD, A. G. GOSLER and W. CRESSWELL*

Edward Grey Institute of Field Ornithology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK; and *School of Biology, Bute Medical Building, St. Andrews University, Fife, KY16 9TS, UK

Summary

1. Individual animals optimize their body mass to enhance fitness and mass is expected to be optimized over both short and long time-scales. On the short time-scale small birds increase mass as they build up energy reserves over each day to avoid starving at night. Theory predicts that starvation risk should be minimized by gaining mass at the start of the day thus insuring against unpredictable food supply later. However, if predation risk is mass-dependent due to reduced escape flight performance, birds should delay mass gain until later in the day to minimize predation risk.

2. Regulation of mass change over longer time-scales has been well documented and a number of studies have been able to show that over weeks, months and years mass is regulated consistent with the starvation–predation risk trade-off being mass-dependent. However, it is crucial to mass-dependent predation theory that it functions over shorter time-scales as well and that birds are able to regulate their diurnal mass gain strategies in response to predation risk. This has not yet been investigated and recent studies of flight performance have been unable to show that small-scale mass change (< 10%) over short time-scales (e.g. diurnal mass change) affects escape flight performance as predicted.

3. We used a unique design of automated identification and weighing system that for the first time allowed the diurnal mass gain of individual great tits *Parus major* to be monitored remotely in the wild. While automatically tracking diurnal body mass changes of individuals we manipulated perceived predation risk by using model sparrowhawks. We were thus able to investigate experimentally the effect of increased perceived predation risk on diurnal mass gain patterns.

4. We show, for the first time, that birds are capable of manipulating their diurnal body mass gain strategy in response to heightened predation risk and that they do so by delaying mass gain until later in the day, as predicted by mass-dependent predation risk theory. Furthermore, the results are consistent with changing flight performance rather than changing exposure time to predators being the driving force for mass-dependent predation risk.

Key-words: diurnal mass change, mass-dependent predation risk, starvation–predation risk trade-off

Introduction

Individual animals optimize their body mass to enhance their chance of survival (Rogers 1987; Rogers & Smith 1993). Theoretical considerations suggest that in winter the energy reserves, and therefore body mass, of small birds should be optimized in terms of the trade-off between starvation risk and mass-dependent predation risk (Houston, McNamara & Hutchinson 1993; Witter & Cuthill 1993; Bednekoff & Houston 1994c). This means that in response to increased starvation risk birds should increase energy reserves, and thus reduce starvation risk, until the benefits of doing so are equal to the costs of increased predation risk due to extra body mass reducing escape flight performance (Houston & McNamara 1993; Bednekoff & Houston 1994b,c). Conversely increased predation risk should
result in an individual reducing body mass to an optimal level that will minimize mortality from both starvation and predation.

It has long been known that birds increase energy reserves in winter (Baldwin & Kendeigh 1938; Van Balen 1967; reviewed Witter & Cuthill 1993), and detailed models based on empirical data have shown that this increase in mass is related to predictors of starvation risk, such as decreasing temperature, decreasing day length, geographical location and dominance status (Gosler 1996; Cresswell 1999). It has recently been shown that over longer time-scales (weeks, months and years) small birds adjust body mass and energy reserves in response to increased predation risk and that they do so by reducing mass in the manner predicted if predation risk is mass-dependent (Gosler, Greenwood & Perrins 1995; Adriaensen et al. 1998; Gentle & Gosler 2001).

A central prediction of starvation–predation risk trade-off theory under mass-dependent predation is that in addition to optimizing mass over longer time-scales birds should adjust their daily mass gain pattern in line with the relative importance of starvation risk and predation risk (Bednekoff & Houston 1994a; McNamara, Houston & Lima 1994; Pravosudov & Lucas 2001). Each day, small birds must build up sufficient energy reserves to survive the night during which they cannot feed but must expend energy to survive (e.g. Gosler 1996; Cresswell 1998; Thomas 2000). Over this short time-scale, theory suggests that starvation risk could be minimized by gaining energy reserves early in the day to insure against the possibility of food being unavailable later in the day, either as the result of some environmental change, such as a sudden snow fall, or because of vagaries in the food supply (Bednekoff & Houston 1994a; McNamara et al. 1994; Pravosudov & Lucas 2001). In contrast, predation risk could be minimized by delaying mass gain until late in the day so that during any predator encounter, escape flight performance (which depends on mass) is maximized (Bednekoff & Houston 1994a; McNamara et al. 1994; Pravosudov & Lucas 2001). To date a small number of studies have shown that birds in aviaries are capable of adjusting their diurnal mass gain in response to food deprivation or manipulated energy expenditure experiments (Bednekoff & Krebs 1995; but not Lilliehökal et al. 1996; Dall & Witter 1998). Thomas (2000) showed that wild robins Erithacus rubecula gain more mass at the start of the day following a reduction in food supply. No published study has yet provided evidence that the rate or trajectory of diurnal mass gain in wild birds responds to changes in predation risk. This is crucial to demonstrating the existence of mass-dependent predation because it is an implicit assumption of the theory that small changes in mass over a short time-scale will give a selective advantage in reducing predation risk that will provide the driving force for larger mass changes to occur over a longer time-scale. Although large-scale changes in mass can be shown to affect escape flight performance (Kullberg, Fransson & Jakobsson 1996; Lind et al. 1999; Krams 2002) recent studies of small-scale diurnal mass change (less than 10%) have been unable to show an effect (Kullberg 1998; Kullberg, Jakobsson & Fransson 1998; Veasey, Metcalfe & Houston 1998; Van der Veen & Lindstrom 2000; Krams 2002). This has lead to suggestions that mass-dependent predation risk based on increased mass reducing flight performance might not be driving the demonstrated link between predation risk and the large-scale longer-term changes in mass (Brodin 2000, 2001). As an alternative it has been suggested that mass-dependent predation risk could be driven by mass-dependent metabolism, which would result in increased exposure to predation risk associated with the requirement to forage more to maintain higher mass (Brodin 2001).

Here we test for the first time for an effect of mass-dependent predation risk on diurnal mass gain trajectories in wild birds. To do so we used a unique design of automated identification and weighing system that allowed the diurnal mass gain of individual great tits Parus major L. to be monitored remotely in the wild without the need for repeated capture at short intervals for weighing, which itself may influence body mass (Gosler 2001). We test the hypotheses that (1) the diurnal mass gain trajectory is a flexible behavioural response that individuals can manipulate in response to changing levels of predation risk, and (2) changes in diurnal mass gain are consistent with mass-dependent predation risk. We predicted that when the perceived predation risk was increased experimentally, mass gain would be delayed until later in the day.

**Methods**

The study was undertaken in the winter of 2001–02 as part of the long-term population study of great tits in Wytham Woods near Oxford, UK (Perrins 1979; Gosler 1993). The experiment manipulated the perceived predation risk at a peanut-feeder site using plastic models of flying sparrowhawks Accipiter nisus L., the main predator of great tits in Wytham. This study builds on the work of Gentle & Gosler (2001) and used the same experimental set-up and location. The work was carried out in a winter with a sparse natural food supply because of a poor beechmast crop and this probably enhanced the attractiveness of the feeder. As part of the long-term study birds were being trapped by mist-nets but the experiment was designed so that trapping level was constant during the study and mist-nets were in use only once at each site in each control and experimental period.

**Individual Identification**

On first capture during the winter each individual was either fitted with a standard metal British Trust for Ornithology (BTO) leg-ring with a unique number or
an existing ring was read. A single colour-ring to which was glued a radio frequency identification (RFID) tag (also known as a PIT, passive integrated transponder, tag) was then fitted. The RFID tag is a tiny rod 12 mm long and 2 mm in diameter, the rod is made of a plastic coating surrounding a ferrite rod antenna and silicon chip, in the presence of the electromagnetic field it produces a unique amplitude modulated code signal. Each bird is thus uniquely identifiable without the need for recapture during the experimental period. A RFID tag weighs 0·1 g, which is approximately 0·5% of the body mass of a great tit in winter and is therefore unlikely to have any significant effect on an individual bird’s behaviour.

AUTOMATED WEIGHING SYSTEM

As birds have been shown to alter their body mass in response to capture, perhaps because they interpret it as a measure of increased predation risk (Gosler 2001), it was important to ensure that the confounding effects of repeated capture could be removed from the experiment. A system was therefore specially designed and built (Francis Scientific Instruments, Cambridge, UK) to weigh individually identified birds without capture each time they visited a feeder. It was designed so that any bird with a RFID tag that landed on the weighing head would be detected and weighed. As weighing accuracy depended on the stability of the load there was a 1-s settling period after the bird landed, then once a stable load was detected the mass was sampled eight times at 1/16th of a second intervals and the mean value was sent to a data logger, mass was measured to the nearest 0·1 g. If the load did not remain sufficiently stable over the sampling period, for example because the bird moved about too vigorously, no mass value was saved. In addition to the mass, the individual bird ID code, the time of the record to the nearest second, the day and the tare weight immediately before weighing were recorded. After 1·5 s the bird was reweighed and another record made for as long as the RFID tag was detected. The system also consisted of a 1·5-m high bird table on which was placed the automated weighing machine so that, when perched on the weighing head, birds could feed from a peanut feeder suspended above and to one side. The bird table was placed between two parallel 1-m² transparent Perspex sheets (30 cm apart) and could be rotated to shelter the weighing system from the wind.

EXPERIMENTAL DESIGN

Four automated weighing machines were installed at feeders at the end of November 2001. Two locations 800 m apart were used; one as a disturbance control and one for the experimental treatment, no great tits moved between these two locations during the experimental period. Each location had two feeders 150 m apart, between which the great tits freely moved. All four sites had similar habitat characteristics in terms of forest structure, cover and exposure to weather. Each site was a small clearing surrounded by mature oak woodland and preliminary General Linear Model (GLM) analysis confirmed neither site nor location resulted in any significant difference in mass. At one site in each location model hawks could be released automatically at randomly chosen times so they swooped out of a box 6 m up a tree, along a length of line, over the feeder and disappeared into another box. The model predator could be replaced by a similarly sized brown plastic bottle which creates a similar level of disturbance but unlike the model is not interpreted by great tits as a predator. By measuring latency of return to feed after exposure to an ‘attack’ by the model predator and bottle, Gentle & Gosler (2001) showed that the model sparrowhawk is perceived as a predator rather than simply a disturbance.

For 3 months prior to the experiments the birds were attracted to the feeders bated with peanuts kernels to familiarize them with the set-up. This period was used to collect baseline mass data. Providing peanut kernels, which are small fragments of peanuts, as bait was important to the success of the experiment because it ensured the birds fed at the feeder long enough to be weighed rather than seizing a single large peanut and retreating to feed in cover. The experiment ran from 2 March to 31 March 2002. At location 1 there was a 10-day pre-experimental control period (A), followed by a 10-day experimental period (B) in which the model sparrowhawk was released three times a day, followed by a 10-day post-experiment control period (C). At location 2 the same procedure was repeated over the same time periods with the plastic bottle released as a disturbance control during the experimental period. Release times were chosen using a random number generator for the hours between dawn and dusk. To avoid the chance of releases being concentrated in a short period of day when few birds might be present release times at least 1 h apart were used.

DATA HANDLING AND ANALYSIS

Over the winter more than 470 000 records indicating the presence of individual birds at the feeders at 1·5-s intervals were collected. These values were aggregated into a single measurement of mean mass for each feeding bout that an individual undertook at a feeder: a 10-min absence from the feeder was used to arbitrarily distinguish between separate feeding bouts. On some occasions birds perched with one foot on the weighing head so that mass was substantially underestimated. To avoid such records influencing the mean mass, we excluded all mass values more than 0·5 g lighter than the maximum mass recorded during a feeding bout, mean mass was calculated only if a feeding bout had at least five valid, repeated mass measurements. Using data from 75 individual great tits a GLM with Individual as a random factor and Time Spent Feeding during
the previous bout as a covariant suggested that an individual’s current mass could not be predicted based on how much it had fed on the last occasion. Feeding behaviour during the previous bout had no significant effect in determining change in mass by the next bout (GLM; Time spent feeding in previous bout, $F_{(4,1497)} = 0.252, P = 0.615$). Therefore mean mass for each bout was treated as an independent measure of an individual’s response to its environment.

We used General Linear Modelling to test our hypotheses, with mass as our dependent variable, and time of day (since dawn), treatment, individual, length of day, day of winter, and five measures of weather as the independent variables plus the interaction between the time of day and treatment. Weather was measured on site by an automatic weather station (Morecroft, Taylor & Oliver 1998). The independent variables controlled for factors known to influence mass change (e.g. Gosler 1996, 2002; Cresswell 1998) and repeated measures from the same individual were controlled for by entering individual into the model as a random factor, while treatment was entered as a fixed factor and represented the difference between the control periods and the treatment period at each location. The interaction term was the focus of our interest as it indicates if the effect of the predation risk treatment on mass, changes over time, i.e. if the diurnal mass gain trajectory is changed by the experiment. In order to determine when during the day any change in diurnal mass gain was occurring we split the day into four equal parts and analysed each part using a separate GLM. We chose to divide the day into quarters because it gave a good balance between the sample size needed to identify effects and the resolution needed to identify when during the day the effects were occurring.

Our first hypothesis tested whether diurnal mass gain trajectory is a flexible behavioural response that individuals can manipulate in response to changing levels of predation risk. We predicted that we would find a significant interaction between treatment and time of day at our experimental location but not at our disturbance control location. Our second hypothesis tested whether changes in diurnal mass gain are consistent with mass-dependent predation risk. We predicted that less mass would be gained in the first parts of the day and more would be gained in later parts of the day.

**Results**

Over the winter 5048 independent mean mass measurements were made from 75 individual great tits (mean number ± SE of feeding bouts per individual 67 ± 11). General Linear Modelling (see Table 1) showed that, in the absence of the experimental treatment, major predictors of mass variation were individual and time of day and that length of day, day of winter, wind speed, rainfall, humidity and mean temperature were also significant predictors of mass variation. The amount of sunshine was not a significant predictor of mass. After controlling for the significant factors other than time of day, Fig. 1 shows that the mean residual diurnal mass gain of $1.1 ± 0.02$ g was uniformly distributed over the day during the winter for the natural level of predation risk at the study site.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>d.f.</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual</td>
<td>2865</td>
<td>70</td>
<td>118</td>
<td>0.001</td>
</tr>
<tr>
<td>Time of day</td>
<td>713</td>
<td>1</td>
<td>2053</td>
<td>0.001</td>
</tr>
<tr>
<td>Day length</td>
<td>183</td>
<td>1</td>
<td>527</td>
<td>0.001</td>
</tr>
<tr>
<td>Day of winter</td>
<td>107</td>
<td>1</td>
<td>309</td>
<td>0.001</td>
</tr>
<tr>
<td>Temperature</td>
<td>1.6</td>
<td>1</td>
<td>5</td>
<td>0.030</td>
</tr>
<tr>
<td>Wind</td>
<td>9</td>
<td>1</td>
<td>25</td>
<td>0.001</td>
</tr>
<tr>
<td>Rainfall</td>
<td>5</td>
<td>1</td>
<td>15</td>
<td>0.001</td>
</tr>
<tr>
<td>Humidity</td>
<td>27</td>
<td>1</td>
<td>77</td>
<td>0.001</td>
</tr>
<tr>
<td>Excluded Sunshine</td>
<td>0.1</td>
<td>1</td>
<td>0.4</td>
<td>0.554</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model</th>
<th>Sum of squares</th>
<th>d.f.</th>
<th>F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Explained</td>
<td>4143</td>
<td>77</td>
<td>155</td>
<td>0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>1327</td>
<td>3822</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>5470</td>
<td>3899</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 1. Normal diurnal mass gain pattern during winter (Dec–Mar) without experimental treatment, residual mass ± 95% confidence interval by quarters of day. Residual mass controlled for individual, day length, day of winter, mean temperature, rainfall, wind and humidity.

The previous bout as a covariant suggested that an individual’s current mass could not be predicted based on how much it had fed on the last occasion. Feeding behaviour during the previous bout had no significant effect in determining change in mass by the next bout (GLM; Time spent feeding in previous bout, $F_{(4,1497)} = 0.252, P = 0.615$). Therefore mean mass for each bout was treated as an independent measure of an individual’s response to its environment.

We used General Linear Modelling to test our hypotheses, with mass as our dependent variable, and time of day (since dawn), treatment, individual, length of day, day of winter, and five measures of weather as the independent variables plus the interaction between the time of day and treatment. Weather was measured on site by an automatic weather station (Morecroft, Taylor & Oliver 1998). The independent variables controlled for factors known to influence mass change (e.g. Gosler 1996, 2002; Cresswell 1998) and repeated measures from the same individual were controlled for by entering individual into the model as a random factor, while treatment was entered as a fixed factor and represented the difference between the control periods and the treatment period at each location. The interaction term was the focus of our interest as it indicates if the effect of the predation risk treatment on mass, changes over time, i.e. if the diurnal mass gain trajectory is changed by the experiment. In order to determine when during the day any change in diurnal mass gain was occurring we split the day into four equal parts and analysed each part using a separate GLM. We chose to divide the day into quarters because it gave a good balance between the sample size needed to identify effects and the resolution needed to identify when during the day the effects were occurring.

Our first hypothesis tested whether diurnal mass gain trajectory is a flexible behavioural response that individuals can manipulate in response to changing levels of predation risk. We predicted that we would find a significant interaction between treatment and time of day at our experimental location but not at our disturbance control location. Our second hypothesis tested whether changes in diurnal mass gain are consistent with mass-dependent predation risk. We predicted that less mass would be gained in the first parts of the day and more would be gained in later parts of the day.

**Results**

Over the winter 5048 independent mean mass measurements were made from 75 individual great tits (mean number ± SE of feeding bouts per individual 67 ± 11). General Linear Modelling (see Table 1) showed that, in the absence of the experimental treatment, major predictors of mass variation were individual and time of day and that length of day, day of winter, wind speed, rainfall, humidity and mean temperature were also significant predictors of mass variation. The amount of sunshine was not a significant predictor of mass. After controlling for the significant factors other than time of day, Fig. 1 shows that the mean residual diurnal mass gain of $1.1 ± 0.02$ g was uniformly distributed over the day during the winter for the natural level of predation risk at the study site.

CHANGES IN DIURNAL MASS GAIN PATTERN

In total, 56 great tits were weighed over the 30 days during which the experiment, pre- and post-controls were conducted and the number of individuals providing mass data in each part of the experiment is shown in Table 2. The graphs in Fig. 2 show that diurnal mass gain was evenly distributed in the pre- and post-experiment
control periods at both locations and during the disturbance control during the experimental period. Figure 2(b) shows that during the experimental treatment the birds responded to the heightened perception of predation risk by delaying mass gain until the last part of the day and did not do so during the disturbance control treatment. Although Fig. 2(b) may appear to have some superficial similarity to Fig. 2(a), the diurnal mass gain in the experimental precontrol period and all other control periods can be modelled by a significant straight line while no such straight line can model diurnal mass gain during the sparrowhawk treatment. Confirming that when perception of predation risk was experimentally increased mass gain at the end of the day increased significantly. The interaction term between time of day and experimental treatment in the GLMs in Table 3 was highly significant, after Bonferroni correction, in the final part of the day ($F_{1,331} = 18.3, P < 0.001$). Consistent with Fig. 2(b) there was also a balancing trend earlier in the day for decreased mass gain, although this was not significant after Bonferroni correction in any individual period. A further four GLMs were run to cover each part of the day at the disturbance control location, the results (not shown in full) indicated that there was a trend for birds to respond to the disturbance control by gaining more mass early in the day. However, after Bonferroni correction the interaction term was never significant (day part 1: $F_{1,74} = 4.0, P = 0.050$. day part 2: $F_{1,231} = 2.8, P = 0.096$. day part 3: $F_{1,375} = 0.1, P = 0.913$. day part 4: $F_{1,194} = 1.9, P = 0.168$. Bonferroni corrected 95% significance level, $P = 0.012$), demonstrating that the birds were not delaying their diurnal mass gain until the end of the day in response to disturbance or as a random response to some external environmental variable such as weather at the time of the experiment.

To demonstrate that the results were due to individual birds adjusting their diurnal mass gain patterns rather than due to different individuals with different behavioural strategies using the feeders during the experimental treatment we reran all eight models only using mass data for the individuals present throughout the trial. Fifteen individual birds (eight at the experimental site and seven at the disturbance control site) were weighed regularly during the pre- and post-experiment controls and during the treatment phase. The pattern of results was identical, with the only significant change in diurnal mass gain being found in the final part of the day at the location during the experimental treatment (model treatment-day part 4: Time of Day*Treatment Interaction, $F_{1,178} = 17.5, P < 0.001$).

<table>
<thead>
<tr>
<th>Location</th>
<th>Period</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (experimental treatment)</td>
<td>n = 24</td>
<td>n = 33</td>
<td>n = 32</td>
<td></td>
</tr>
<tr>
<td>2 (disturbance treatment)</td>
<td>n = 23</td>
<td>n = 18</td>
<td>n = 17</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Sample sizes of individual great tits from which data were collected in each period of experiment.
Table 3. Results of GLMs for each part of day, showing sparrowhawk release significantly increases mass gain trajectory (interaction term) in the final part of the day while over the earlier parts of the day there is a balancing trend towards a decreased mass gain trajectory.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>First quarter of day $R^2 = 0.57$</th>
<th>Second quarter of day $R^2 = 0.72$</th>
<th>Third quarter of day $R^2 = 0.73$</th>
<th>Fourth quarter of day $R^2 = 0.78$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sum of squares</td>
<td>d.f.</td>
<td>$F$</td>
<td>Sig.</td>
</tr>
<tr>
<td><strong>Main effect</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>214.7</td>
<td>28</td>
<td>13.1</td>
<td>0.001</td>
</tr>
<tr>
<td>Time of day</td>
<td>5.1</td>
<td>1</td>
<td>8.7</td>
<td>0.003</td>
</tr>
<tr>
<td>Day length</td>
<td>4.1</td>
<td>1</td>
<td>7.1</td>
<td>0.008</td>
</tr>
<tr>
<td>Temperature</td>
<td>12.2</td>
<td>1</td>
<td>20.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Wind</td>
<td>2.8</td>
<td>1</td>
<td>4.8</td>
<td>0.029</td>
</tr>
<tr>
<td>Rainfall</td>
<td>1.9</td>
<td>1</td>
<td>3.3</td>
<td>0.070</td>
</tr>
<tr>
<td>Humidity</td>
<td>0.0</td>
<td>1</td>
<td>0.0</td>
<td>0.910</td>
</tr>
<tr>
<td>Day of winter</td>
<td>4.2</td>
<td>1</td>
<td>7.1</td>
<td>0.008</td>
</tr>
<tr>
<td>Treatment</td>
<td>2.9</td>
<td>1</td>
<td>4.9</td>
<td>0.027</td>
</tr>
<tr>
<td><strong>Interaction</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment* time of day</td>
<td>1.6</td>
<td>1</td>
<td>2.7</td>
<td>0.101</td>
</tr>
<tr>
<td><strong>Model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Explained</td>
<td>283.6</td>
<td>37</td>
<td>13.1</td>
<td>0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>171.7</td>
<td>293</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>455.3</td>
<td>330</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

†The parameter estimate was positive indicating that more mass was gained during experimental treatment.
Discussion

During nonexperimental periods, great tits increased their mass more or less linearly through the day, as had been demonstrated from observations made on captured birds (e.g. Gosler 1996). However, great tits delayed their diurnal mass gain until the latter part of the day when perceived predation risk was increased experimentally; in contrast there was no detectable change in diurnal mass gain pattern in response to the disturbance control treatment.

This is the first demonstration that individual wild birds optimize their mass gain strategy over the short-term (the hours of a single day) in response to predation risk, which is one of the central predictions of starvation–predation risk trade-off theory (Bednekoff & Houston 1994a; McNamara et al. 1994; Pravosudov & Lucas 2001). That the birds respond to the sparrowhawk model but not the disturbance control by delaying their diurnal mass gain shows that the birds were not responding to the predator simply as an interruption to foraging brought about by disturbance (McNamara et al. 1994; Lilliendahl 1998). Indeed as both the predator and disturbance treatments occurred randomly through the day, interrupted foraging would not be expected to produce any consistent change in the diurnal mass gain pattern. Instead the results are as predicted by the mass-dependent predation risk hypothesis where flight performance (or possibly foraging exposure) is expected to deteriorate as mass increases and so birds should respond to a heightened perception of predation risk by delaying their essential mass gain until the end of the day (Bednekoff & Houston 1994a; McNamara et al. 1994).

Of the two hypothesis proposed to explain the mass-dependence of predation risk, the hypothesis that mass change is linked to predation risk via reduced flight performance as mass increases, clearly predicts that our results should show a delay in mass gain until later in the day (Bednekoff & Houston 1994a; McNamara et al. 1994). In contrast it is not clear why mass-dependent predation risk caused by greater mass increasing basal metabolic rate and therefore prolonging foraging exposure to predators (Brodin 2001), would produce the demonstrated delay in diurnal mass gain. After taking an increased foraging risk and gaining the mass required to survive until the next day woodland birds such as the great tit can take advantage of the refuge effect (Cresswell 1998) by seeking cover and using it as a refuge to wait out the rest of the day with the minimum possible energy expenditure. Therefore, the way that they gain mass during the day is unlikely to be related to the level of predation risk. Even if the birds were to remain active throughout the day the extra mass-dependent metabolism costs for flight due to extra mass are predicted by Brodin's models to have 'hardly any visible effects' on the daily mass gain curves (Brodin 2001). According to Brodin's models what might create a mass-dependent metabolism cost sufficient to increase predation risk and make it mass-dependent is an increase in basal metabolic rate overnight. Such an increase is suggested to be possible due to an increase in energetically expensive muscle to help a heavier bird maintain its escape flight performance (Brodin 2001). However, such compensatory changes in muscle size are known to take several days (Witter, Cuthill & Bonser 1994; Lind & Jakobsson 2001; Kullberg, Metcalfe & Houston 2002), and would not be fast enough to compensate for diurnal mass gain and overnight mass loss, which happen alternately over, on average, 12-h periods. Therefore, there seems to be no obvious selective advantage why birds facing increased predation risk due to the hypothesized mass-dependent metabolism, should increase their starvation risk by delaying diurnal mass gain until later in the day. The random timing of the release of the sparrowhawk models over the whole day meant that there was no incentive for birds to feed later in the day to avoid predators and previous work suggests that sparrowhawks may actually be more active later in the day during winter (Van der Veen 2000). The evidence from this study, showing that diurnal mass gain patterns respond in line with a mass-dependent predation risk cost, suggests that changes in flight performance due to small short-term changes in mass, although they have not yet been demonstrated, are biologically significant and need to be investigated further experimentally.

By manipulating overnight energy expenditure, Lilliendahl et al. (1996) showed that great tits under experimental aviary conditions are capable of responding to increased starvation risk by shifting diurnal mass gain to early in the day. It has also been shown that under natural conditions wild blackbirds Turdus merula and robins Erithacus rubecula gain mass most quickly early in the day when starvation risk is relatively high (Cresswell 1998; Thomas 2000). Having shown in this study that in their natural environment great tits are capable of waiting until the final part of the day to gain most of the energy reserves required to survive the overnight fast, it seems reasonable to assume that they should also be capable of foraging intensively at the start of the day to gain most of their body mass early on if it were advantageous to do so. Instead as Fig. 1 shows, in winter the great tits at Wytham normally adopt a constant pattern of diurnal mass gain. Interpreting the diurnal mass gain graph in terms of starvation–predation trade-off theory suggests that great tits in Wytham are faced neither with a high starvation risk nor with a high predation risk during the winter. This is consistent with the ecology of the great tit; it is a large and therefore dominant tit species giving it reliable access to available food (Gosler 1996; Gosler & Carruthers 1999) and like other arboreal foragers, it has a relatively reliable food supply (Rogers & Smith 1993). Previous work suggested that on average great tit flocks at Wytham encounter only one sparrowhawk a day (Morse 1973) a much lower level than our experimental manipulation used to produce the delay in diurnal mass gain.
The findings of our study indicate that examining diurnal mass gain patterns may provide a useful measure of how birds perceive the relative starvation and predation risks of their environment, something that is otherwise very difficult to determine (Cresswell 2003). We suggest that diurnal mass gain patterns could be used as a convenient and inexpensive conservation tool when there is a need to identify whether population declines are being caused by reduced survival due to food supply problems. For example, this technique might be applied to the conservation problem of declining farmland birds in Britain to test whether species declines are being caused by a reduced food supply due to agricultural intensification (Krebs et al. 1999; Siriwardena, Baillie & Wilson 1999).

In conclusion, diurnal mass gain strategies are a flexible behavioural response that individuals can manipulate in response to changing levels of predation risk. These strategies respond to the experimental heightening of perceived predation risk as predicted by theoretical models of the starvation–predation trade-off and this study provides unique evidence to support the existence of mass-dependent predation risk.

Acknowledgements

We gratefully acknowledge the help and expertise of Mike Francis whose work on the detailed design and construction of the automated weighing and detection system was essential to the success of the study. Thanks to John Quinn and Mark Whittingham for many helpful discussions and to Henk van der Jeugd, Phil Barnett, Ben Sheldon and Simon Griffith for help with ringing the birds and general advice. Meteorological data were provided by the NERC Centre for Ecology and Hydrology and were collected under the UK Environmental Change Network programme. During this study RM was supported by a NERC studentship, WC by a Royal Society University Research Fellowship and AGG by the University of Oxford.

References


Received 20 July 2004; accepted 17 March 2005