How climate change might influence the starvation–predation risk trade-off response

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Climate change within the UK will affect winter starvation risk because higher temperatures reduce energy budgets and are likely to increase the quality of the foraging environment. Mass regulation in birds is a consequence of the starvation–predation risk trade-off: decreasing starvation risk because of climate change should decrease mass, but this will be countered by the effects of predation risk, because high predation risk has a negative effect on mass when foraging conditions are poor and a positive effect on mass when foraging conditions are good. We tested whether mass regulation in great tits (*Parus major*) across the UK was related to temporal changes in starvation risk (winter temperature 1995–2005) and spatial changes in predation risk (sparrowhawk *Accipiter nisus* abundance). As predicted, great tits carried less mass during later, warmer, winters, demonstrating that starvation risk overall has decreased. Also, the effects of predation risk interacted with the effects of temperature (as an index of foraging conditions), so that in colder winters higher sparrowhawk abundance led to lower mass, whereas in warmer, later, winters higher sparrowhawk abundance led to higher mass. Mass regulation in a small bird species may therefore provide an index of how environmental change is affecting the foraging environment.

Keywords: mass-dependent predation risk; starvation risk; interrupted foraging; great tit; mass

1. INTRODUCTION

Understanding how starvation risk is affected by environmental change, controlling for predation risk, should allow us to better predict how animal populations will change in the future. This is because the starvation–predation risk trade-off provides a framework to predict the behaviour, fitness, population dynamics and community structure of animals (Abrams 1984; McNamara & Houston 1987; Bolker *et al.* 2003; Cresswell 2008). Starvation risk should be affected greatly by environmental change, such as global warming, because ambient temperature is a major factor influencing starvation risk, particularly for temperate birds in winter (Lima 1986; McNamara *et al.* 1994). Higher temperatures reduce energy budgets (Calder & King 1974), affecting prey activity and accessibility, daily energy needs and the costs of foraging (e.g. Grant *et al.* 2000; McGowan *et al.* 2002; Sergio 2003; Yasue *et al.* 2003), and so are likely to improve the quality of the winter foraging environment (Schaefer *et al.* 2006; Wrona *et al.* 2006; Wiegand *et al.* 2008).

Changes in starvation risk affect mass in birds because as starvation risk increases (i.e. foraging becomes more unpredictable) birds increase their reserves of stored energy as insurance for when foraging gain is less than energy needs (Rogers 1987; Pravosudov *et al.* 1997; Cresswell 1998). Birds do not always maintain high energy stores, however, because energy reserves are costly (Witter & Cuthill 1993) both in terms of the extra foraging time needed to acquire the extra reserves and to maintain them, because fatter birds have higher

metabolic rates, all other things being equal (Houston *et al.* 1997). There is also a cost in terms of predation risk because a fatter bird will have to spend more time foraging and therefore exposed to predation risk (Brodin 2001). Mass may also increase the predation risk because fatter birds accelerate more slowly when taking flight and so are likely to be less able to initially outrun attacking predators such as sparrowhawks, *Accipiter nisus* (e.g. Kullberg *et al.* 1996).

Mass in birds is therefore a consequence of a trade-off between starvation and predation risk (Houston & McNamara 1993; Houston *et al.* 1993; Bednekoff & Houston 1994). Therefore, if the effect of predation risk is controlled for (or is acting equally), mass of an individual bird provides an index of the relative importance of starvation risk and so the quality of the foraging environment (Lima 1986; MacLeod *et al.* 2007). Birds should therefore respond to good foraging environments, all other things being equal, by reducing their mass.

Although mass increases the predation risk in birds, mass can be gained or lost in response to increased risk of predation depending on the overall level of starvation risk (Lima 1986; Houston *et al.* 1993; Witter & Cuthill 1993; McNamara *et al.* 2005; MacLeod *et al.* 2007). When starvation risk is low, individuals can optimize their survival in response to an increased density of predators by choosing to forage under conditions where attack is unlikely or unlikely to be successful. Restricting foraging to safe times and places ('interrupted foraging'), however, increases the foraging unpredictability (Lima 1986). Birds can therefore respond to this increased risk of starvation by increasing the mass (e.g. Lilliendahl 1998). In contrast, when starvation risk is high, individuals cannot waste time or energy restricting their foraging

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opportunities to avoid any potential attack by a predator. As they must continue to forage under risk of attack by a predator, birds optimize their probability of survival on attack by reducing their mass, so reducing their overall foraging time and risk of attack, and improving their escape performance if they are attacked (Witter & Cuthill 1993). Therefore, in good foraging environments, birds should respond to increased predation risk by increasing the mass and in poor foraging environments by decreasing the mass.

In this paper, we test whether mass regulation in great tits, as a consequence of the starvation–predation risk trade-off, is related to improvements in the foraging environment, as measured by increases in winter temperatures over a 10-year period. Great tit (*Parus major*) mass has been shown to decrease with decreased starvation risk (Gosler 1996; Gosler & Carruthers 1999), increased predator abundance (Gosler *et al.* 1995) and increased predator attack rate (Gentle & Gosler 2001), and recent papers have established that great tits can show both mass gain (MacLeod & Gosler 2006) and loss (MacLeod *et al.* 2005b) in response to predation risk, which is likely to be dependent on environmental conditions (MacLeod *et al.* 2007).

Starvation–predation risk trade-off theory with respect to mass regulation in birds predicts that increasing the starvation risk will always increase the mass, but this may be countered by the effects of predation risk, because a high predation risk has a negative effect on mass when foraging conditions are poor and a positive effect on mass when foraging conditions are good (figure 1). We therefore predict that when the effects of predation risk are controlled for, great tits will show relatively lower over winter average mass in recent, milder winters. However, in response to higher predation risk in any one winter, great tits will have a lower mass in a severe winter and will have a higher mass in a milder winter. There should therefore be a positive correlation between change in mass in response to predation risk with temperature across winters.

2. MATERIAL AND METHODS

We measured mass from great tits captured for ringing. The birds in the study were ringed in the winters of 1995–1996 to 2004–2005 as part of the British and Irish Ringing Scheme, organized by the British Trust for Ornithology: ringing data from England, Scotland and Wales were used. The study focused on mass variation outside the breeding season so that body mass would not be influenced by changes owing to reproduction. To effectively exclude breeding birds, we used only capture records between November and February (Wernham *et al.* 2002). For each first capture of an individual, age (first winter or second winter and older), sex, ring number, date, time and location of capture were recorded and standard measurements of wing length to 1 mm and mass to 0.1 g were made (Redfern & Clark 2001). Maximum air temperature, minimum air temperature, mean air temperature, day length and time since sunrise for each capture were obtained or calculated from data provided by the NERC British Atmospheric Data Centre or via the website of the Astronomical Applications Department of the US Naval Observatory (for details, see MacLeod *et al.* 2005a). The dataset of mass measurements from 26 219 individual

birds (each sampled only once) allowed us to identify whether mass was changing in response to hawk abundance (see below), and whether this change depended on year, controlling for important confounding variables that also affect starvation risk and therefore mass. The confounding variables considered were: body size (as measured by wing length, age and sex, with mass increasing with wing length and age, and greatest for males), month (mass increases during the winter with mass being greatest in November and December), day length (mass decreases with day length), latitude (mass increases with latitude in the UK), longitude (mass decreases with longitude in the UK) and time of day (mass increases with time of day) (Cresswell 1998; MacLeod *et al.* 2007).

We estimated the predation risk by estimating sparrowhawk abundance. Sparrowhawks are the main avian predator of birds in Britain (Newton 1986) and frequently eat great tits (Cresswell 1995). Sparrowhawk density (Gosler *et al.* 1995) as well as their presence or absence experimentally (Gentle & Gosler 2001; MacLeod *et al.* 2005b) has been shown to affect the body mass of great tits.

We estimated hawk abundance from sparrowhawk breeding distribution data. Starvation–predation risk trade-off theory makes its predictions based on the individual's perceived risk of predation, which unlike overall proportion of predation mortality in the population is dependent on the presence of predators, or predator abundance, rather than on the ratio of predator to prey density (Lima 1986; Lima & Dill 1990; Abrams 1993; Houston & McNamara 1993). We therefore used sparrowhawk breeding abundance data for 10 × 10 km squares of the UK (Gibbons *et al.* 1993) as a measure of the predation risk environment in the area of capture. Within 10 × 10 squares, there are 25 2 × 2 km squares (tetrads), and the presence or absence of sparrowhawks is recorded in each tetrad. We used the proportion of tetrads in which sparrowhawks were recorded as an index of sparrowhawk abundance within the area encompassed by the 10 km square (i.e. 0.8 means that sparrowhawks were recorded in 20/25 tetrads). The proportion of 10 km squares occupied by hawks varied from 0 to 0.75 (0.13 ± 0.005) and varied significantly with longitude (less abundant in the east -0.10 ± 0.003 , $F_{1,619} = 8.6$, $p = 0.003$) but not latitude ($F_{1,619} = 1.5$, $p = 0.22$): overall model $R^2 = 0.01$ considering the $N = 622$ 10 km² where great tits were sampled.

It is important to note that these data come from breeding data collected in 1988–1991 and so there is a clear temporal mismatch between our mass data and the predator abundance data. We believe that these breeding season data are a reasonable representation of sparrowhawk status at the time of the study because sparrowhawks have (after a decline owing to pesticide pollution) had a stable distribution in Britain since reaching their population and distribution maximum by about 1990 (Snow & Perrins 1998). In addition, populations at carrying capacity are relatively stable (Newton & Rothery 2001), sparrowhawks in the UK remain on their breeding territories year round (Newton 1986) and are sedentary with mostly short range dispersal by young (Newton 1975). In any case, these data represent the most accurate data available, but sparrowhawk abundance and distribution may have changed somewhat during the period of mass data (1996–2004). We also do not consider other predators that may be important, such as feral cats (e.g. Woods *et al.* 2003). However, such errors should not introduce systematic bias into the analysis and

Figure 1. How starvation risk and predation risk might combine to change mass in great tits as temperature increases. As the temperature increases, so less mass is put on as insurance against starvation during winter (1. solid and dotted lines main graph). But the effects of temperature interact with predation risk so that where hawk abundance is high, and winter temperatures are low (2. inset graphs: mass decreases with hawk abundance), mass is lowered (so average mass is decreased from the solid line to the dotted line). But where hawk abundance is high, and winter temperatures are also high (3. inset graphs: mass increases with hawk abundance), mass is increased (so average mass is increased from the solid line to the dotted line). For example, starvation risk (low temperature) may add +1 g and predation risk remove −0.5 g, so overall the bird is fatter because of starvation risk, but not as fat as it would be in the absence of predation risk.

should only increase the probability of obtaining a type II error because they introduce noise into the data that might have masked the underlying pattern.

We estimated yearly average winter temperature from weather station data collected over the same spatial and temporal scale over which mass measurements of great tits were taken. Temperature data for each year were taken from a single weather station within each of 40 British regions (usually counties). Which weather station data were used within a county was determined by choosing the weather station closest to where most individual great tits were caught in that region. Eighteen regions did not have great tit mass samples in all of the 10 years and so temperature data for these regions were excluded to prevent any temperature changes with time being confounded by any systematic spatial variation in great tit sampling through time. The maximum, minimum and mean daily temperatures for each day, for every region in the UK that provided mass samples in each year of the whole 10-year period ($n = 40$) were recorded, and the mean for each of the three temperature measurements was then calculated for each winter. Using the mean of the mean daily temperature, maximum daily temperature or minimum daily temperature gave similar results in all analyses, as might be expected, because the three measures were highly correlated (minimum Pearson's correlation = 0.82, $p < 0.003$, $N = 10$ years): the mean daily temperature was therefore used in all analyses as representative of overall daily temperature. When temperature data were used from all 58 regions where great tit mass data were collected, instead of 40, the results were very similar in terms of both biological and statistical significance.

General linear modelling was used to investigate the effects of year (10 years as a factor) and higher or lower predation risk (hawk abundance as a covariate), on the body mass of great tits. Mass data were normally distributed. We controlled for the effects of month (four-level factor, November–February), body size (wing length and sex), dominance (age), day length and time of day by including these variables in each model (Cresswell 1998; MacLeod *et al.* 2005a). We controlled for spatial autocorrelation by including longitude and latitude of capture in all models. We checked for nonlinear effects of spatial autocorrelation by including latitude, latitude squared, longitude, longitude squared and longitude $\times$ latitude and found that the hawk parameter estimate was not significantly different comparing the simple spatial models (that considered spatial data linearly) with the models considering spatial data in a more complicated and nonlinear way. We therefore selected the simple spatial model as the most parsimonious approach to incorporating spatial data.

Although we sampled individual birds, our analyses are at the level of individual year means because we are testing whether mass responses to the same predation risk each year are different between years. Our sampling unit to test our hypotheses is therefore $N = 10$ years. We therefore use general linear models (GLMs) to derive the relationships between mass and hawk abundance for each year separately (either by separating years or by considering year as a main effect with the interaction term year $\times$ hawk abundance in datasets that pool years), while statistically controlling for the effects of all potential confounding variables (i.e. effectively statistically creating the condition 'all other things being equal'). We then analyse how the parameter estimates

(which are either relative mean differences in mass for different years or relative gradients of the relationship between hawk abundance and mass for each year) change across the 10 years or across the mean temperature values associated with each year. Note that we test for changes in mass with changing temperature conditions or year sequence (climate change) by correlating across years. For changes with respect to predation risk, however, our predation risk data do not vary with year. Therefore, we test for effects first spatially, within years: we determine the degree of mass change with varying hawk abundance across the UK for each year. We then compare each year's value of degree of mass change caused by hawks to look for consistent differences in the effects of the constant predation risk with annual temperature variation or systematically through time. Finally, we also correlated mean temperature with year using linear regression, to confirm that winters have become warmer recently and so to test an assumption for our predictions.

3. RESULTS

The average winter mass of great tits over the 10-year period was 18.6 ± 0.01 g ($N = 26\,219$ great tits measured during the study, which encompasses the period of highest annual mass for great tits). The amount of mass carried by great tits over the winter has become significantly less in recent winters when controlling for a number of confounding variables to allow for comparison between years of unequal spatial and temporal sampling (month, hawk abundance, sex, age, wing length, latitude, longitude, hours of daylight and day length; figure 2). Considering the raw data only, great tits weighed, on average, 18.78 ± 0.03 g ($N = 1471$) in the first two winters, compared with 18.54 ± 0.01 g ($N = 8273$) in the last two winters of the study. There was a significant negative correlation between the parameter estimates for year (from the model as in table 1 without the interaction term) and year sequence ($F_{1,8} = 24.1$, $R^2 = 0.72$, $p = 0.001$, $B = -0.025 \pm 0.005$; figure 2) with an overall decrease of about 0.25 g or 1.5 per cent of the average winter mass over the 10-year period.

Whether great tit mass was higher or lower in areas where hawks were more abundant was significantly different depending on the year (table 1). The biological significance of the effect of spatial variation in hawk abundance on mass in great tits within each year is shown in figure 3: controlling for the other variables, hawk abundance probably caused great tits to carry either lower or higher mass, depending on the year, over a range of 1.3 g. This mass range represents a change in about 7 per cent of the average mid-winter mass. It should be noted that most of the effect is in the first two years of the study, where predation risk responses were associated with lower mass, although in the last few years, predation risk responses were associated with the highest levels of mass. Mass was more likely to be lower during cold winters and higher during warm winters where there was increased hawk abundance (linear regression of the parameter estimates for year $\times$ hawk abundance interaction from the model in table 1, with mean annual winter temperature: $F_{1,8} = 13.4$, $p = 0.006$, $R^2 = 0.58$, $B = 0.15 \pm 0.042$; figure 4).

On average, mass was more likely to be higher where there was greater hawk abundance in later years, and

Figure 2. Residual mass of great tits during the winter with year. The mean of residuals (± 1 s.e.) were plotted from a GLM of mass with month as a factor, and hawk abundance, sex, age, wing length, latitude, longitude, hours of daylight and day length as covariates. The illustrated change is significant ($F_{1,8} = 24.7$, $p = 0.001$, $R^2 = 0.73$; $B = -0.023 \pm 0.005$).

more likely to be lower in earlier years (linear regression of the parameter estimates of year $\times$ hawk abundance interaction—from the model in table 1 and illustrated in figure 3—with year: $F_{1,8} = 12.4$, $p = 0.008$, $R^2 = 0.56$, $B = 0.11 \pm 0.032$). Average winter daily temperature also increased significantly with year (linear regression of average daily temperature with year: $F_{1,8} = 59.8$, $p < 0.001$, $R^2 = 0.87$; figure 5).

4. DISCUSSION

We showed that great tits now carry less mass on average during the winter period: the decrease in mass was equivalent to 1.5 per cent of overall winter mass or 23 per cent of average winter diurnal mass gain (see MacLeod *et al.* 2005b) and so is likely to be biologically significant. We also showed that great tits' mass was predicted by sparrowhawk abundance, with mass being lower or higher with increased sparrowhawk abundance depending on which year was considered, and that this variation was probably due to variation in the mean temperatures (and so the severity of the winter) in different years. Great tits shifted their responses in areas of higher numbers of predators from carrying low mass to carrying higher mass as temperatures became warmer through the study period. The increase in mass was equivalent to 7 per cent of overall winter mass or 118 per cent of average winter diurnal mass gain (see MacLeod *et al.* 2005b) and so, again, is likely to be biologically significant.

Although our results are clear, they are correlational and based on the assumption that predation risk did not change systematically with increasing year. But we are reasonably confident that sparrowhawk abundance has not changed systematically over the period of 1994–2007, which encompasses the period of our study, because there has been no significant change in UK Breeding Bird Survey index for sparrowhawks (index = -12 , 95% CL -24 to $+1$, Baillie *et al.* 2009). We are also reasonably confident that population sizes of sparrowhawks in Britain have not changed substantially

Table 1. Predictors of winter mass in great tits over a 10-year period.

dependent variable: mass source	type III				parameter estimates
	sum of squares	d.f.	<i>F</i>	significance	
corrected model	18 686.2	29	754.1	<0.001	
intercept	56.4	1	66.0	<0.001	
wing length	2274.6	1	2661.9	<0.001	0.17 ± 0.003
sex	1657.8	1	1940.0	<0.001	male 0.65 ± 0.01
age	3.4	1	3.9	0.048	first winter −0.026 ± 0.01
longitude	788.4	1	922.7	<0.001	−0.12 ± 0.004
latitude	172.5	1	201.9	<0.001	0.062 ± 0.005
day length	187.2	1	219.1	<0.001	−0.0001 ± 0.00001
time of day	3442.3	1	4028.4	<0.001	0.0001 ± 0.00001
year	80.9	9	10.5	<0.001	
month	97.9	3	38.2	<0.001	^a
hawk abundance ^c	0.2	1	0.3	0.61	
year × hawk abundance	18.3	9	2.4	0.011	^b
error	22 378.5	26 189			
total	9 106 690.6	26 219			
corrected total	41 064.7	26 218			
adjusted <i>R</i> ² = 0.45					

^aNov: 0.14 ± 0.024; Dec: 0.10 ± 0.036; Jan: −0.026 ± 0.03; Feb: reference.

^bPlotted in figure 2.

^cNote that the main effect of hawk abundance cannot be assessed because it forms part of a significant interaction: if the model is run without the interaction term, then higher hawk abundance (on average over all years) has a strong positive effect on mass ($F_{1,26198} = 11.5$, $p = 0.001$, $B = 0.17 \pm 0.05$).

since the beginning of the 1990s (see Gibbons *et al.* 1993; Crick *et al.* 1998; Baker *et al.* 2006), so our index of abundance from 1989–1991 is likely to be representative of abundance through our study until 2005. Our conclusions also depend on starvation risk not decreasing systematically with year owing to factors other than changes in the mean winter temperature. These factors might include increases in availability of winter food, for example, through increases in supplemental feeding (e.g. O’Leary & Jones 2006). Although great tit populations have increased throughout the period of the study (Baillie *et al.* 2009), there are no data currently available to test whether natural food supply for great tits or supplemental feeding has also increased systematically in Britain. Annual relative visitation rate of great tits to British gardens, where supplemental feeding of great tits occurs has, however, remained constant from 1995 to 2009 (<http://blx1.bto.org/gbw-dailyresults/results/gbwr437-20.html>, accessed 6 May 2009), suggesting that food supplies in gardens are perhaps not driving population increases.

It seems likely that the flexibility of mass regulation shown here—shifting from lower mass to higher mass in response to increased sparrowhawk abundance dependent on foraging conditions—is general in small birds. For example, in an analysis across the 30 most commonly ringed small bird species in Britain, one-quarter carried lower mass in response to higher hawk abundance, whereas half carried higher mass, with several species showing either lower or higher mass dependent on whether their populations were declining or increasing, respectively (MacLeod *et al.* 2007). In this analysis, mass was correlated with populations change as a proxy of environmental conditions (MacLeod *et al.* 2007) rather than directly with a measure of environmental change as in this study.

In this study, because of limited power ($N = 10$ years), we have considered only a linear function to link average temperature with mass response. The data, as illustrated in figure 2, may, however, suggest a step function, and qualitative reasoning also suggests that this is a possibility. Because mass gains in response to increased predation risk (interrupted foraging effects) have only recently been widely empirically demonstrated (MacLeod *et al.* 2007) and flexibility in response to the environment is shown for the first time in this study, there are not yet explicit theoretical predictions about how mass response will be linked to measures of starvation risk. However, qualitatively we would predict that there could be a step function linking starvation risk with mass. This is because as the quality of a good foraging environment starts to decline (i.e. temperature falls), more fat is needed as short-term insurance for the increased unpredictability of foraging for any given level of hawk ‘disturbance’ (Lima 1986; Houston *et al.* 1993). More mass should then be gained as the quality of the foraging environment declines until a bird is forced to reduce its time avoiding hawks in order to forage to sustain its long-term energy budgets. At the point when a bird cannot spare any time avoiding a hawk, fat reserves become a liability—exposing the foraging bird to increased risk of capture and increasing exposure time to maintain the reserves (Witter & Cuthill 1993). At this point, it seems likely that a bird should switch to a strategy where mass is minimized. Figure 3 does suggest a shift in response type at a mean winter temperature of 0.5°C, but not that the highest mass for the interrupted foraging response is immediately after the shift in response as predicted by our qualitative model. Further research is needed to elucidate the exact shape of the function.

Our results provide an interesting footnote to one of the original mass-dependent predation hypothesis

Figure 3. The amount of mass gained or lost for great tits as abundance of sparrowhawks increases for 10 different winters 1994–1995 to 2004–2005. The model shown in table 1 was run (excluding year and the year $\times$ hawk abundance interaction) for each year of the study separately, and the parameter estimate for hawk abundance ± 1 s.e. are plotted. A reference line where hawk abundance had no effect on mass on average is plotted; points below the line show years where greater hawk abundance led to decreases in mass and above where greater hawk abundance led to increases in mass. That some points lie well above and below this line indicates that the effect of hawk abundance differs depending on year (illustrating the significant interaction of year $\times$ hawk abundance in the model in table 1).

Figure 4. Mass gain or loss in response to higher hawk abundance plotted with mean daily temperature for the 10 winters of the study. Mass gain or loss was taken as the parameter estimates for the year $\times$ hawk abundance interaction for the model in table 1: note the values use 2004–2005 as the reference value. A dotted reference line where hawk abundance had no effect on mass on average is plotted: that points consistently lie below this line at low temperatures, and above at higher temperatures, illustrates the likely significant interaction of hawk abundance with temperature.

papers of Gosler *et al.* (1995), which showed that mass of great tits across England was greater during winters when sparrowhawks were absent in accordance with the hypothesis that increased predation risk should decrease mass in birds. Data for the absence of sparrowhawks come from the 1950s to 1960s in Wytham Woods, Oxfordshire, when winter temperatures were much colder than recently ($F_{2,55} = 7.6$, $p = 0.001$; 1950s

Figure 5. Change in mean daily winter temperature with year.

and 1960s $B = -1.1 \pm 0.29^\circ\text{C}$; 1970s and 1980s $B = -0.61 \pm 0.29^\circ\text{C}$; 1990s to present reference category; comparing yearly means of November–February monthly average minimum temperatures from Oxford (<http://www.metoffice.gov.uk/climate/uk/stationdata/oxforddata.txt> accessed 26 June 2008). When winters are colder, we predict mass loss with increased hawk abundance, and so an increase in mass in their absence, as was observed by Gosler *et al.* (1995). But with warmer winter temperatures of recent years, we predict that if sparrowhawks were again to become absent from Wytham Woods, great tits would show a decrease in winter mass (assuming that density-dependent effects, which will also affect starvation risk, are the same now). Our results show that shifts from mass loss in response to predation risk to mass gain in response to hawk abundance can probably occur between years and we predict that such shifts are likely to occur even within winters, dependent on temperature and/or foraging conditions.

This study demonstrates how mass in birds may change with climate change by reducing absolute starvation risk for a temperate bird species in winter as well as changing its capacity to compensate for predation risk. Empirical work described above, and theoretical models, have demonstrated that mass gain in response to predation risk is likely to be an advantageous strategy associated with favourable foraging conditions (e.g. McNamara *et al.* 2005; Brodin 2007) and thus increasing populations (MacLeod *et al.* 2007). As winter temperatures increase, great tits can afford to avoid predators in time and space, can afford to carry higher fat loads despite the increased metabolic costs they entail and, if foraging conditions suddenly become worse (i.e. a sudden cold spell), they have greater fat reserves as insurance. The results of this study also suggest that mass in birds, when controlling for predation risk, can provide an indication of the quality of the foraging environment. For example, if birds show low mass in the presence of predators, it suggests that the foraging environment is poor. Similarly, if birds in an area that have previously shown high mass in the presence of predators start to show lower mass on average, without changes in temperature or hawk abundance, then this would suggest that the quality of the foraging environment has decreased.

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