

Body mass change strategies in blackbirds *Turdus merula*: the starvation–predation risk trade-off

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Summary

1. It is theoretically well established that body mass in birds is the consequence of a trade-off between starvation risk and predation risk. There are, however, no studies of mass variation from sufficiently large wild populations to model in detail the range of diurnal and seasonal mass change patterns in natural populations and how these are linked to the complex environmental and biological variables that may affect the trade-off.
2. This study used data on 17 000 individual blackbirds *Turdus merula* to model how mass changes diurnally and seasonally over the whole year and over a wide geographical area. Mass change was modelled in respect of temperature, rainfall, day length, geographical location, time of day and time of year and the results show how these mass changes vary with individual size, age and sex.
3. The hypothesis that seasonal mass is optimized over the year and changes in line with predictors of foraging uncertainty was tested. As theory predicts, reduced day length and reduced temperature result in increased mass and the expected seasonal peak of mass in midwinter.
4. The hypothesis that diurnal mass gain is optimized in terms of starvation–predation risk trade-off theory was also tested. The results provide the first empirical evidence for intraspecies seasonal changes in diurnal mass gain patterns. These changes are consistent with shifts in the relative importance of starvation risk and predation risk and with the theory of mass-dependent predation risk.
5. In winter most mass was gained in the morning, consistent with reducing starvation risk. In contrast, during the August–November non-breeding period a bimodal pattern of mass gain, with increases just after dawn and before dusk, was adopted and the majority of mass gain occurred at the end of the day consistent with reducing mass-dependent predation risk. The bimodal diurnal mass gain pattern described here is the first evidence that bird species in the wild gain mass in this theoretically predicted pattern.

Key-words: blackbird, diurnal mass gain, energy reserves, mass change, mass-dependent predation.

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Introduction

In animals, increased body mass can increase survival and reproductive success through the availability of stored energy reserves as insurance against unpredictable foraging opportunities (Owen & Black 1989; Houston & McNamara 1993; Bednekoff & Houston 1994b;

Gosler 1996; Thomas 2000). Yet animals, particularly birds, usually maintain considerably lower body mass than the maximum possible (Cresswell 1998; Van Balen 1967; Witter & Cuthill 1993; Gosler 1996). This is theoretically predicted to be the result of mass-dependent costs (Witter & Cuthill 1993; Bednekoff & Houston 1994b): most notably in birds, mass-dependent predation due either to body mass having a detrimental effect on the ability to take off quickly and escape from predators or to the increased foraging time necessary to maintain a greater mass (Bednekoff 1996; Kullberg, Fransson & Jakobsson 1996; Brodin 2000, 2001;

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Krams 2002; Kullberg, Metcalfe & Houston 2002b). Body mass is therefore the subject of a trade-off between the risk of starvation and the risk of predation, so that fitness is maximized (Lima 1986; Houston & McNamara 1993; Houston, McNamara & Hutchinson 1993; Gosler, Greenwood & Perrins 1995b).

Theoretical models of the starvation–predation risk trade-off in birds predict that seasonal and diurnal mass should follow specific patterns of mass change (McNamara & Houston 1990; Houston & McNamara 1993; Houston *et al.* 1993; McNamara, Houston & Lima 1994). Rather than constantly aiming to minimize starvation mortality by maintaining maximum possible energy reserves (and therefore maximum body mass), birds should optimize their body mass at a lower level so that the overall mortality from starvation and predation is minimized (King 1972; King & Murphy 1985; Rogers 1987; Rogers & Smith 1993; Bednekoff & Houston 1994b). Optimum body mass will therefore vary seasonally depending on the relative importance of starvation risk and predation risk. Body mass would be expected to increase in winter when energy requirements are highest, because of longer and colder nights, and foraging opportunities at the most unpredictable (Rogers 1987; McNamara & Houston 1990; Bednekoff & Houston 1994b). For diurnal mass gain the null hypothesis, known as the risk-spreading theorem, is that mass should be gained evenly over the day (Houston *et al.* 1993; McNamara *et al.* 1994). Instead, trade-off theory predicts that birds should alter their diurnal mass gain pattern in response to the relative importance of starvation and predation risk (McNamara *et al.* 1994). By foraging intensively at the start of the day and storing up energy reserves early, a bird will be able to minimize the chance of starving due to foraging opportunities not being available later in the day, e.g. because of snowfall, disturbance or random variation in the food supply. In contrast, by leaving foraging until the end of the day, an individual can avoid carrying around mass that will reduce its escape ability if it encounters a predator and, thus, reduce its predation risk for most of the day.

The theory of this trade-off has been investigated in detail and a few experimental studies have shown that actual or perceived perception of predation risk results in reduced body mass (e.g. Lilliendahl 1997, 2000; Cresswell 1999; Gentle & Gosler 2001). In order to test if the predictions of the trade-off hold in natural systems, detailed empirical data on natural changes in body mass are needed to model how body mass responds to the interaction of the multiple biotic and environmental conditions that occur in the wild.

Wide variation in the body mass of birds has been documented over many years, both by observations in the field and during experimental studies under captive conditions (e.g. Baldwin & Kendeigh 1938; Van Balen 1967; Bednekoff, Biebach & Krebs 1994; Smith & Metcalfe 1997; Thomas & Cuthill 2002). Yet there is still a paucity of detailed empirical data on how body mass changes in response to multiple factors and

therefore a lack of data to support the theoretical model predictions on how mass should change and how this should influence behaviour (Houston & McNamara 1993; Houston *et al.* 1993; Witter & Cuthill 1993; McNamara *et al.* 1994). Existing studies in the wild have often tracked mass change in a small population at a single location and usually lack predictive power due to insufficient sample size when dealing with the large number of potentially influential factors. Alternatively, studies are experimental, based on captive birds on an artificial feeding regimen and kept under far from natural conditions with regard to light, cover and exposure to weather. As the experiments and controls are performed under the same artificial conditions, this need not be a problem for the study of specific behaviours. However, captive conditions can give contradictory results regarding mass change (e.g. Lilliendahl 1998; van der Veen & Sivars 2000), making it difficult to use the results to predict mass change in natural systems.

Studies examining the isolated effect of an individual factor or a small number of factors on fat reserves or body mass have shown an inverse relationship with temperature and day length and a positive relationship with body size, time of day, rainfall, snowfall and wind (e.g. Waite 1992; Pilastro, Bertorelle & Marin 1995; Gosler & Carruthers 1999; Thomas 1999). However, a review of the literature reveals only two studies using modern modelling techniques that have had sufficient data to model the complex of factors influencing mass change in wild birds. Gosler (1996) studied winter fat storage, which is correlated strongly with body mass, in a population of great tits *Parus major* and found four factors (time of day, mean temperature, social status and day length) were significant in explaining fat score. Cresswell (1998) provided a field study of individual blackbirds *Turdus merula* that had sufficient sample size to document the extent of mass change in individuals and demonstrate a significant effect of size, month, day length, temperature and year on mass variation during winter.

The current study follows on from that work and aims, by using empirical data collected from all over Britain, to quantify, model and explain patterns of mass change over the entire year and over a wide geographical range. For the blackbird *T. merula* this study tests two main hypotheses: first, that seasonal mass is optimized over the year and changes in line with predictors of foraging uncertainty, such as decreasing temperature and day length. Based on starvation–predation risk trade-off theory we predicted that reduced day length and temperature would result in increased mean body mass and that these factors would produce the expected seasonal peak of mass in winter. Secondly, we test the hypothesis that diurnal mass gain is optimized over the day, rather than being gained in the roughly constant pattern explained by a constant intensity of foraging in line with the risk-spreading theorem (Houston *et al.* 1993). We predicted that diurnal mass gain patterns would change at different times of the year in response to alterations in the relative risk of starvation and predation.

Table 1. Results of linear regressions examining how well individual temperature variables predict variation in body mass. Sample size based on number of ringing records with data for each temperature variable on day of ringing (maximum possible $N = 17\,774$)

Independent variable	Max. air temp.	Min. air temp.	Mean air temp.	Min. grass temp.	Min. soil temp. at 10 cm depth
N	16 997	16 921	16 876	14 912	11 840
R^2	0.187	0.135	0.180	0.091	0.206
P	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Independent variable	Previous day's min. air temp.	Previous day's max. air temp.	5-day mean of max air temp.	5-day mean of min air temp.
N	16 877	16 994	16 904	16 714
R^2	0.134	0.187	0.208	0.174
P	< 0.001	< 0.001	< 0.001	< 0.001

Methods

RINGING AND BIOMETRIC DATA

This study uses data collected by volunteer British Trust for Ornithology (BTO) bird ringers, as part of the national bird ringing scheme for Britain and Ireland (Redfern & Clark 2001). Since 1995 ringers have, on a voluntary basis, entered ringing data onto computer in a standard format; this now makes up the BTO computerized ringing database which provided the data for this study. In total, data from the first capture of 17 744 individual blackbirds between September 1995 and March 2000 were used. For each capture, ring number (unique to the individual), date, location, age and sex were recorded and standard measurements of wing length to 1 mm and mass to 1 g were made (Svensson 1992; Redfern & Clark 2001). The age of birds was classed as first-year or adult, with birds classed as adult after they had moulted at the end of their first breeding season. Only records with valid data for all the preceding fields were used, and because it is a separate land mass no captures from Ireland were included. Additionally, time of ringing was available for 15 302 of the records. Under the BTO ringing scheme each ringer trains with other experienced ringers for at least 1 and usually 2 years before they receive a licence. Standard measurements are therefore reasonably consistent across the country and repeatable (Gosler *et al.* 1995a; Gosler *et al.* 1998). In any case, with thousands of individual ringers taking measurements it is expected that any errors will be normally distributed and thus there will be no bias in measurements due to multiple observers.

WEATHER DATA

Daily weather data collected by British Meteorological Office weather stations for 67 British counties between 1996 and 2000 were downloaded from the database held by the NERC British Atmospheric Data Centre (BADC 2002). By calculating the mean ringing location of all birds ringed in that county and then choosing

the weather station, with the required data, closest to that point, representative weather data were chosen for each county. Due to equipment failure or a lack of measurements for some of the more remote parts of Britain there are some days in some counties that lack data for some weather variables. The weather variables for which daily data were collated were: rainfall, maximum air temperature, minimum air temperature, minimum grass temperature and minimum soil temperature at 10 cm depth (see Table 1 for sample sizes). Additionally the current day's mean temperature, the previous day's minimum and maximum air temperatures and the 5-day mean of the minimum and the maximum air temperatures were calculated. Grass and soil temperatures are measured at weather stations less frequently than the air temperatures therefore gaps in the original data meant it was not considered worthwhile to attempt to calculate 5-day means for these variables.

SUNRISE AND SUNSET DATA

Daily sunrise and sunset times for each day in each county between 1996 and 2000 were calculated using procedures of the United States Naval Observatory. These were accessed via the website of the Astronomical Applications Department of the Naval Observatory (AAD 2002). By entering the mean ringing location for the chosen county and the year annual tables of sunrise and set times were produced for each of the 67 counties.

DATA ANALYSIS

A database was produced for analysis that linked the data from each ringing record with the weather data, sunrise and sunset times for the county on that day. This allowed the length of daylight on day of ringing and the time since dawn of ringing to be calculated.

Before analysing the effect of weather on mass, the extent of correlation between different weather variables and geographical location was tested for. All nine temperature variables showed large and significant

Table 2. Results of minimum adequate general linear model of factors predicting mass variation, produced by reverse stepwise regression. Dependent variable is mass, $N = 13\,935$ individual blackbirds, adjusted $R^2 = 0.40$

Source of variation	Sum of squares	d.f.	<i>F</i>	Sig.
Main effects				
Wing length	46 518	1	793.3	< 0.001
Month	30 847	11	47.8	< 0.001
Time of day	12 690	1	216.4	< 0.001
Mean max. temp (5-day)	11 884	1	202.7	< 0.001
Day length	7 666	1	130.7	< 0.001
Year	5 619	4	24.0	< 0.001
Distance North	642	1	10.9	0.001
Rainfall	576	1	9.8	0.002
Age	382	1	6.5	0.011
Sex	289	1	4.9	0.026
Distance East	281	1	4.8	0.029
Two-way interactions				
Sex × month	9 196	11	14.3	< 0.001
Sex × mean max. temp	886	1	15.1	< 0.001
Sex × age	288	1	4.9	0.027
Age × month	3 679	11	5.7	< 0.001
Age × rainfall	571	1	9.7	0.002
Age × daylight	312	1	5.3	0.021
Month × time of day	2 234	11	3.5	< 0.001
Day length × mean max. temp	5859	1	99.9	< 0.001
Model				
Explained	541 310	62	148.9	< 0.001
Residual	813 419	13 872		
Total	1 354 728	13 934		
Non-significant interactions dropped from model				
Sex × rain	3	1	0.0	0.82
Sex × day length	0	1	0.0	0.95
Sex × time of day	14	1	0.2	0.63
Sex × year	252	4	1.1	0.37
Age × mean max temp	7	1	0.1	0.73
Age × time of day	26	1	0.4	0.51
Age × year	408	4	1.7	0.14
Sex × month × age	1 139	11	1.8	0.05
Sex × month × year	216	4	0.9	0.45

correlations with each other (Pearson's correlation: $r_p > 0.6$, $P < 0.05$). All other variables showed only small correlations between themselves and with the temperature variables (Pearson's correlation: $r_p > 0.3$, $P < 0.05$). On this basis, the effects of different temperature variables on mass were examined by individual linear regressions. The best predictor of mass was the 5-day mean of the maximum air temperature preceding capture ($R_{16\,904}^2 = 0.208$, $P < 0.001$), followed closely by minimum soil temperature at 10 cm depth ($R_{11\,840}^2 = 0.206$, $P < 0.001$); Table 1 shows other variables. As well as having marginally greater predictive value, the 5-day mean of maximum air temperature had a much greater sample size available and was therefore the temperature variable selected for use in the main analysis. These two variables (5-day mean of maximum air temperature and minimum soil temp) were highly correlated (Pearson's correlation coefficient = 0.892, $P < 0.001$, $N = 11\,512$).

Data analysis was performed using the SPSS statistical programs (Norusis 1998; SPSS 2001). The main method of analysis was general linear modelling and all

models illustrated are minimum adequate models produced by reverse stepwise regression. On the basis of the significant factors in the initial models (see Tables 2 and 3) and biological information on the timing of breeding, etc. (Snow & Perrins 1998), the year was divided into three periods to simplify further modelling (winter = December, January and February; breeding = April, May, June and July; non-breeding = August to November; March was excluded because, depending on weather and geographical location, this month can either provide winter conditions or be part of the breeding season).

Means are presented in the form mean ± standard error. When presenting results graphically the authors have chosen to present actual mean mass rather than displaying residuals of mean mass after controlling for variance due to factors such as location. The seasonal and diurnal patterns illustrated in the results using actual mean mass are the same as those found when the authors plotted residual mean mass (e.g. see Fig. 1). The benefit in presenting results as actual rather than

Table 3. Significant predictors of variation in mass for each month. Results of 12 general linear models, run for each month separately based on main factors from minimum adequate model in Table 2. Black squares very highly significant $P < 0.001$, grey squares highly significant $P < 0.01$, *significant $P < 0.05$, ? lack of significance due possibly to small sample size in that month. With Bonferroni correction, black and grey squares are significant at $P < 0.05$

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>n</i>	1064	890	671	540	808	696	802	861	626	3592	2297	1088
Wing length												
Time of day				*		*						
Year												
Mean max. temp		*					*					
Day length						*						
Distance North				?			*	*				
Distance East									*			
Rainfall	*					*						
Sex						*						
Age												
Mass variance explained (%)	26	26	30	21	16	18	19	18	9	12	15	24

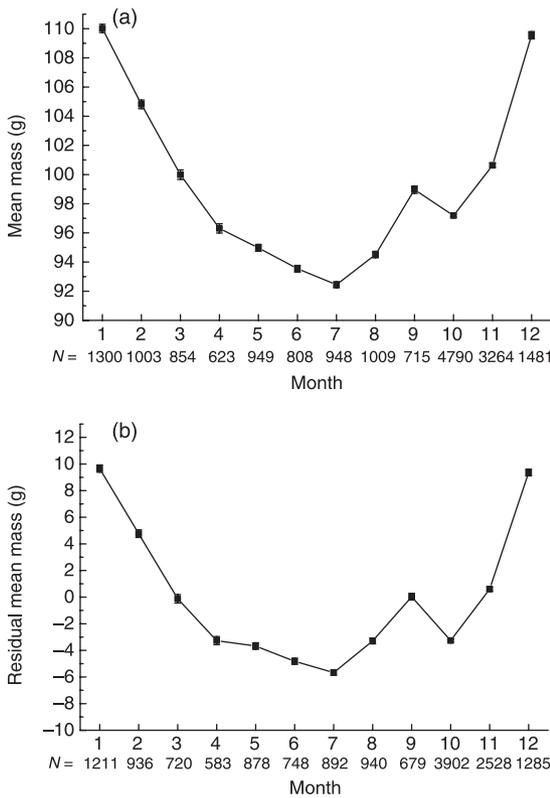


Fig. 1. Annual cycle of variation in mass: (a) actual mean mass; (b) residual mass after controlling for all significant non-seasonal factors in the model shown in Table 2.

residualized mean mass is that actual mass is more biologically significant and easier to interpret. When presenting diurnal mass graphs representing differences in mass gain over the course of the day, the day was divided into five equal parts, with the hours of daylight split into sections representing the first fifth, second fifth, etc. from dawn. We chose to divide the day into fifths rather than smaller or larger parts because it gave a good balance between the sample sizes needed to look at effects and the resolution needed to identify when during the day the effects were occurring. Similar

Table 4. Mean mass (g) results by age and sex class

Age and sex classes	<i>N</i>	Mean mass	SD	Min. mass	Max. mass
First-year male	6115	99.9	9.7	71	148
First-year female	5981	97.9	9.3	73	142
Adult male	2517	102.8	10.4	76	150
Adult female	3131	100.3	9.9	72	141

patterns were obtained when the day was divided into quarters or tenths.

Results

MASS VARIATION IN THE POPULATION

For 99.9% of blackbirds ringed in Britain between 1995 and 2000 mass lay between 71 and 150 g and mean mass was 99.7 ± 0.1 g ($n = 17\,744$, data exclude 0.1% of measurements at extremes of range which are represented by single measurements that may be errors). Mean mass varied with age and sex, as shown in Table 4; males were significantly heavier than females (mean difference = 2.1 ± 0.2 g, $t_{17\,056} = 14.0$, $P < 0.001$) and adults were significantly heavier than first-year birds (mean difference = 2.4 ± 0.2 g, $t_{10\,401} = 15.1$, $P < 0.001$). Some of this variation in mass was a result of size differences: adult males (mean wing length = 134.6 ± 0.1 mm) were larger than first-year males (mean wing length = 131.5 ± 0.1 mm); these in turn were larger than adult females (mean wing length = 129.6 ± 0.1 mm) which were larger than first-year females (mean wing length = 128.1 ± 0.1 mm). Figure 2 uses wing length as a measure of body size (Gosler *et al.* 1998) to show the positive linear relationship between mass and size. Using linear regression, 8.3% of the variation in mass was explained by wing length (wing length² and wing length³ explained identical amounts of variation in mass). The general linear model presented in Table 2 shows that size, represented by wing length, was the

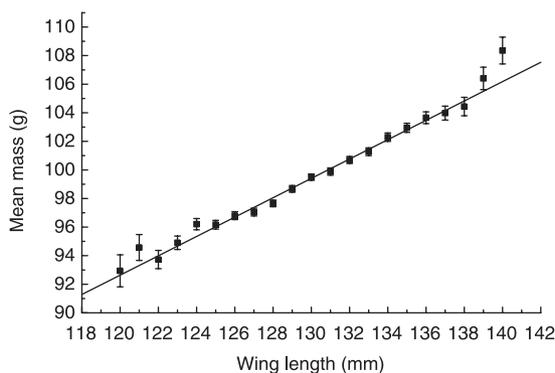


Fig. 2. Variation in mean mass with size (measured by wing length). Line fitted by linear regression: $R^2 = 0.08$, $Y = 0.706X + 7.65$, $T_{17743} = 1601.1$, $P < 0.001$.

best predictor of mass variation over the entire year. Due to a strong interaction with the month of the year, age and sex both predicted only very small amounts of variation over the whole year; after taking account of the other factors in the model, males are marginally heavier than females and adults marginally heavier than first-year birds. After controlling for all other factors, geographical location of capture (in terms of distance north and east in Britain) was a significant but very small predictor of mass variation. In general, linear regression shows that blackbirds became heavier further north ($R^2 = 0.011$, $F_{1,17742} = 197.4$, $P < 0.001$) and increase marginally in mass from west to east ($R^2 = 0.001$, $F_{1,17742} = 10.5$, $P < 0.001$).

SEASONAL CYCLE OF MASS VARIATION

The GLM in Table 2, which explains 40% of variation in mass, shows that time of year represented by month of capture was an important predictor of mass variation. Figure 1 shows how the mean mass of blackbirds varied during the year and that this pattern of mass change remained when using residual mean mass after controlling for all the factors which do not vary seasonally (age, sex, size, time of day, year, distance north and east). Higher than average mass was maintained from November to February, with the peak in January (mean mass = 110.0 ± 0.3 g) and lower than average from April to October with the minimum in July (mean mass = 92.4 ± 0.2 g). The pattern is similar during the winter months for the different sex and age classes, but as shown by the significant interactions of month with sex and age the pattern changes in summer. Figure 3a shows that females were significantly heavier than might otherwise have been expected when egg laying in April, May and June. Figure 3b shows that adult birds were significantly heavier than birds starting their first year during the fledging period of May to August.

We reran the minimum adequate general linear model separately for each month to examine in more detail which factors were important at different times of the year; Table 3 shows which factors were signifi-

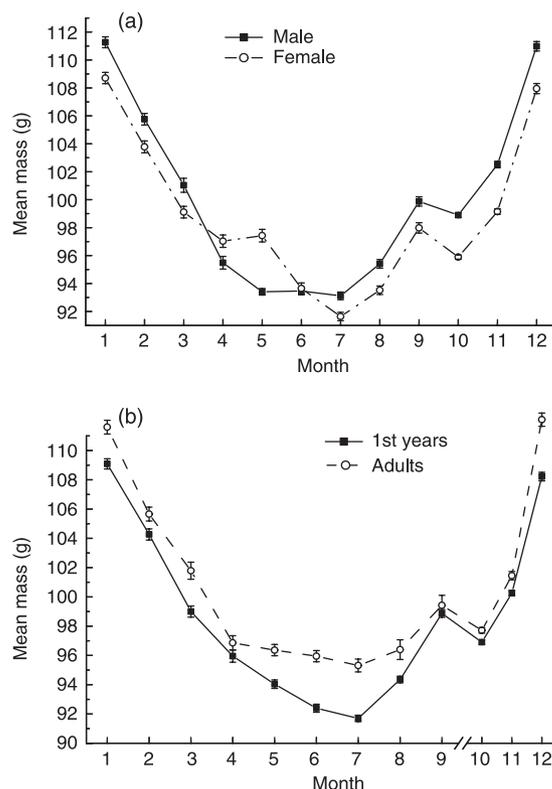


Fig. 3. Annual cycle of variation in mean mass; (a) by sex; (b) by age class. The break in the x-axis between September and October indicates the change in age class from first-year to adult as birds complete their first year of life.

cant in each month. Size was the major predictor of mass in every month while sex was significant only in the breeding season (March–June) and during the migration months of October and November. As already suggested in Fig. 3b, age is principally a significant predictor of mass in the post-fledging months of May, June, July and August; however, it is again significant in midwinter.

DIURNAL VARIATION IN MASS

Over the day, blackbird mean mass varied from 99.0 ± 0.2 g one hour after dawn to 103.4 ± 0.4 g during the ninth hour from dawn. A similar percentage of diurnal change occurred at all times of the year with the absolute value of mean mass varying by month as described in Fig. 1a. Table 3 shows a strong relationship between time of day and mass for all months except July. There was no significant interaction between time of day and age or sex but the pattern of mass change over the day is significantly different at different times of the year as indicated by the month \times time of day interaction in the model (Table 2). Figure 4 illustrates how mean mass varied over the day during three parts of the year. In winter (December–February), mass was lowest in the first fifth of the day, had increased sharply by the third fifth and was then maintained over the rest of the day before being lost

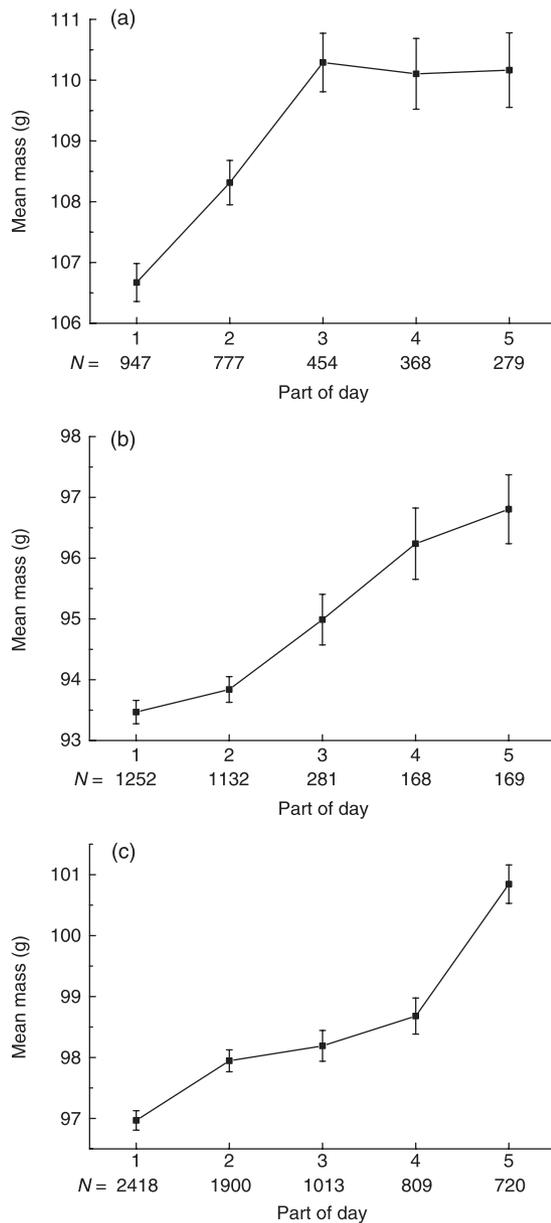


Fig. 4. Diurnal variation in mean mass; (a) during winter (December–February), showing mass gain early in the day; (b) during the breeding season (April–July), showing mass gain over the whole day; (c) during the non-breeding season (August–November), showing bimodal mass gain at the start and end of the day. The time period is in fifths of the day.

during the overnight fast. During the breeding season (April–July) mass was lowest before dawn and increased fairly steadily over the whole day. During the non-breeding season (August–November) birds were lightest in the first fifth, had increased mass sharply by the second fifth, slowly increased or maintained mass from the second to fourth periods and then gained mass fastest in the final part of the day. When dividing the day into fifths there was insufficient sample size to run separate GLMs for each part of the day to examine how mass was affected by time of day. However, dividing the day into thirds and controlling for the same factors as in Table 3 allowed us to run GLMs for each part of

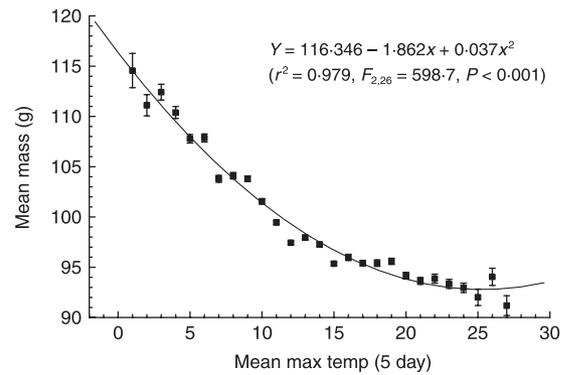


Fig. 5. Variation of mean mass against temperature ($^{\circ}\text{C}$). $R^2 = 0.979$, $Y = 0.037 \times 2 - 1.862X + 116.346$, $F_{2,26} = 598.7$, $P < 0.001$.

the day and confirmed that the patterns illustrated in Fig. 4 were significant. In winter, time of day had a significant effect on mass only in the first third of the day (first part: $F_{1,1312} = 8.5$, $P = 0.004$; second part: $F_{1,722} = 0.7$, $P = 0.414$; third part: $F_{1,445} = 0.0$, $P = 0.873$) while, in contrast, time of day was a highly significant predictor of mass change in both the first and last thirds of the day but not in the middle, during the non-breeding season (first part: $F_{1,3462} = 21.7$, $P < 0.001$; second part: $F_{1,1744} = 0.3$, $P = 0.596$; third part: $F_{1,1108} = 14.0$, $P < 0.001$). There was insufficient sample size in the latter part of the day to conduct the same analysis for the breeding season period.

MASS VARIATION AND WEATHER EFFECTS

Figure 5 illustrates the inverse relationship between the 5-day mean of the maximum air temperature and mass, the quadratic form of this relationship indicates that above a threshold temperature there will be no further reduction in mass. The general linear model in Table 2 shows that the 5-day mean of maximum air temperature and rainfall are the two weather variables that are best predictors of mass variation.

Discussion

MASS VARIATION IN THE POPULATION

British blackbirds showed considerable variation in mean body mass both seasonally (19%) and diurnally (4.5%). Forty per cent of mass variation was predicted by size, time of year (represented by month), time of day, year, day length, geographical location, weather (represented by 5-day mean of maximum air temperature preceding capture and rainfall on day of capture), age and sex. Patterns of mass variation changed at different times of the year according to age and sex and different diurnal mass gain strategies were adopted according to season. The grouping of months in which factors were significant, shown in Table 3, suggests that it is the period within the annual cycle of the bird that is important.

A GLM similar to Table 2 that used period in place of month still explained 38% of mass variation.

Size is well known as a good predictor of body mass (Gosler *et al.* 1998) and as expected it was the best predictor in this study. The seasonal changes in the importance of sex in determining body mass suggest increased mass-dependent predation risk as a cost of breeding for female blackbirds, as has been shown in recent studies of blue tits *Parus caeruleus* and pied flycatchers *Ficedula hypoleuca* (Kullberg, Houston & Metcalfe 2002a; Kullberg *et al.* 2002b). Another potential explanation of the greater mass of females in the breeding season could be that they are responding to a reduced predation risk resulting from being less conspicuous and that body reserves can be increased to reduce starvation risk. However, as the breeding season is a time of high food availability, starvation risk should be low and it seems unlikely there would be any significant drive for females to carry increased fat reserves at this time of year. Body mass in the first months after fledging was significantly lower than for adults, indicating that blackbirds leave the nest before achieving the mass they maintain as adults. In species such as the blackbird that have open nests, such a strategy which reduces time in the nest is likely to be adaptive, both in reducing vulnerability to nest predators (Hatchwell, Chamberlain & Perrins 1996a,b; Cresswell 1997) and in decreasing mass-dependent predation risk during the period in which young birds develop flight skills.

SEASONAL CYCLE OF MASS VARIATION

In blackbirds, the yearly cycle of mass change (Fig. 1) shows the classic pattern of winter fattening predicted by starvation–predation risk trade-off theory (Lima 1986; McNamara & Houston 1990; Houston & McNamara 1993; Bednekoff & Houston 1994b). As predicted, maximum mass is reached in December and January when the combination of long winter nights and cold temperatures means birds require the greatest fat reserves to survive the overnight fast. The seasonal pattern shown here, where blackbirds are able to maintain their maximum mass when foraging time is shortest and food availability is lowest, supports the hypothesis that a bird's energy reserves are optimized in line with predictors of foraging uncertainty. The alternative hypothesis, that a bird's body mass is limited by food availability, is not supported as this would lead to peak mass when food availability is greatest during the autumn berry crop. Energy reserves therefore seem to be under behavioural control with the bird responding strategically to environmental conditions in order to minimize the combination of starvation and predation mortality (Witter & Cuthill 1993). Cresswell (1998) showed that, over the course of a single winter, individual blackbirds were capable of increasing mass up to 143% of their minimum mass, indicating that the mean mass variation pattern found in this study is likely to be explained by individual birds strategically controlling their mass.

DIURNAL VARIATION IN MASS

The different diurnal mass gain strategies (Fig. 4) found in different periods of the year provide evidence that birds are capable of adapting their diurnal mass gain strategy in line with the predictions of risk trade-off theory (McNamara *et al.* 1994). Bednekoff & Houston (1994a) have predicted that mass-dependent predation risk should result in species adopting a bimodal diurnal mass gain pattern in order to reduce predation mortality. Although McNamara *et al.* (1994) summarized eight studies that showed some evidence for an increased amount of foraging at dawn and dusk, until now there was little convincing evidence for bimodal diurnal mass gain occurring under natural conditions. The results presented here show that, in the post-breeding period when blackbirds have an abundant food supply in the form of both invertebrates and ripening berries (Snow & Perrins 1998), they gain mass in a bimodal pattern (Fig. 4c). Following overnight mass loss, birds forage early in the day, gaining approximately one-third of the mass lost during the previous night's fast. They then forage minimally in the middle of the day and gain the remaining two-thirds of their required energy reserves in the final part of the day. By adopting this strategy, birds avoid carrying extra mass for most of the day and they should therefore increase their chance of survival on encountering a predator, by being able to fly faster and/or being more manoeuvrable. This delay in mass gain provides less support for the idea that the effect of mass on predation risk rather than being directly linked to reduced flight performance may instead be the result of increased predation risk due to the increased foraging time necessary to gain extra mass. If increased time exposed to predators were the main force driving mass-dependent predation there would be little advantage to birds delaying mass gain until later in the day, as this would not alter the time exposed to predators.

In contrast, during the winter blackbirds adopt a diurnal strategy of rapidly gaining mass during the first half of the day. Theoretically, this should result in starvation risk being minimized (Bednekoff & Houston 1994a; McNamara *et al.* 1994). Cresswell (1998) found a similar morning mass gain pattern in his study of individual blackbirds. He interpreted this pattern of early morning fattening as being the result of blackbirds being able to escape predation risk, when not foraging, by using dense bushes as a refuge from predators, as predicted by Houston *et al.* (1993). The refuge effect is a refinement of the starvation–predation risk trade-off theory that allows an animal to escape to a zero predation risk environment. Thus, allowing them to avoid the costs of mass-dependent predation that would otherwise make it optimal to restrict total mass and gain mass later in the day. Here the winter diurnal mass gain strategy of rapid early morning mass gain is consistent with the refuge effect. However, there is no similar effect of concentrated early morning

mass gain in the non-breeding period. As the refuge effect would be expected to function in both periods this suggests that the winter strategy is explained better by starvation risk in winter increasing relative to predation risk, resulting in a diurnal strategy that is optimized in terms of starvation risk reduction. In winter the weather can deteriorate rapidly, snowfall can hide food or a drop in temperature can reduce invertebrate availability while increasing the energy reserves necessary to survive the night. Under such variable conditions the optimum strategy appears to be to gain energy reserves, and therefore mass, as early and as quickly as possible. The resultant increase in predation risk is traded-off against the risk of starvation due to uncertainty in food availability.

The diurnal mass gain strategy is different again in the breeding season. During this period, when birds are trying to maximize their reproductive success, the starvation–predation risk trade-off no longer seems to drive mass gain behaviour. Instead, birds forage and gain mass through the entire day. This apparently continuous diurnal mass gain is consistent with the risk-spreading theorem (Houston *et al.* 1993) which predicts that, when mass-dependent effects are unimportant and interruption to foraging (by adverse weather conditions, etc.) is negligible, birds should spread out their mass gain and risk taking over the whole day. Considering that seasonal mass variation far exceeds diurnal mass variation, it seems reasonable that the relatively small diurnal mass gains in summer should have little effect on birds that are able to deal with much higher mass loads through the winter (Cresswell 1998).

MASS VARIATION AND WEATHER EFFECTS

Local weather, particularly temperature, is a major factor in determining how much weight and therefore energy reserves blackbirds carry. Due to the high correlation between the different temperature variables we chose to use only the strongest predictor of mass variation in our modelling. This predictor was the mean maximum air temperature calculated over the 5 days leading up to capture, but it is important to note that this is very highly correlated with the minimum soil temperature at a depth of 10 cm. Considering that blackbirds forage principally on the ground for soil-living invertebrates, whose activity will be linked to soil temperature, we believe it likely that the birds are responding to this, rather than the mean maximum air temperature. Although we could not separate the effects of these two variables, the analysis showed clearly that they are both considerably better predictors of mass variation than measures of minimum air temperature, mean air temperature and grass temperature. In contrast, Gosler (1996) found great tits respond most strongly to mean air temperature. It seems reasonable that, although in general low temperature and other correlated poor weather conditions will affect energetic costs and foraging of all birds, spe-

cies with different foraging strategies will respond to different measures of temperature as a consequence.

In conclusion, body mass in blackbirds is a highly variable property that is controlled in response to multiple biological and environmental factors. The empirical evidence presented here supports two important predictions of how body mass is optimized in relation to starvation–predation risk trade-off theory. First, it suggests that under normal winter conditions in Britain the energy reserves carried by most individuals are not limited by the abundance of food. This conclusion is supported by the observation that birds can maintain their highest energy reserves at the poorest time of year for foraging (represented by coldest temperatures and shortest foraging time). Further support is provided by the fact that during this period birds can rapidly gain all their required energy reserves in half the available foraging time. Secondly, it appears that, in winter, birds are optimizing mass in a way that deals with the problems of a variable food supply and a less predictable environment that result in a higher starvation risk relative to the predation risk; while, in autumn, birds are adopting a diurnal mass gain strategy consistent with reducing predation risk when starvation risk is low. Both strategies are consistent with the predictions of mass-dependent predation risk theory and optimizing mass in line with trading off the relative importance of predation risk and starvation risk at different times of the year.

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