LETTER

Mass regulation in response to predation risk can indicate population declines

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Abstract

In theory, survival rates and consequent population status might be predictable from instantaneous behavioural measures of how animals prioritize foraging vs. avoiding predation. We show, for the 30 most common small bird species ringed in the UK, that one quarter respond to higher predation risk as if it is mass-dependent and lose mass. Half respond to predation risk as if it only interrupts their foraging and gain mass thus avoiding consequent increased starvation risk from reduced foraging time. These mass responses to higher predation risk are correlated with population and conservation status both within and between species (and independently of foraging habitat, foraging guild, sociality index and size) over the last 30 years in Britain, with mass loss being associated with declining populations and mass gain with increasing populations. If individuals show an interrupted foraging response to higher predation risk, they are likely to be experiencing a high quality foraging environment that should lead to higher survival. Whereas individuals that show a mass-dependent foraging response are likely to be in lower quality foraging environments, leading to relatively lower survival.

Keywords

Interrupted foraging, mass-dependent predation risk, starvation risk.

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INTRODUCTION

In theory, survival rates and consequent population status might be predictable from instantaneous behavioural measures of how animals prioritise foraging vs. avoiding predation (Lima 1986; Lemon 1991; Houston *et al.* 1993; Rogers & Smith 1993; Olsson *et al.* 1999, 2002). Except when risk of starvation is high and imminent, anti-predation behaviours tend to be of more immediate importance in the trade-off between the need to forage and the need to avoid predation (Lima 1986; Houston *et al.* 1993; Witter & Cuthill 1993). Theoretically, this means that the degree to which animals prioritize foraging over anti-predation behaviour should indicate starvation risk, which will reflect the environmental quality of their habitat (Lemon 1991; Olsson *et al.* 2002; MacLeod *et al.* 2006).

In birds, mass can provide an index of the trade-off between predation and starvation risk (Lima 1986; Bednekoff & Houston 1994). This is because birds with higher fat reserves (and so higher mass) can survive longer periods of unpredictable foraging (Rogers 1987). Increased mass, however, reduces a bird's ability to accelerate quickly at take-off or when flying away from an attacking predator and/or requires more time exposed to predators while foraging to create and maintain the extra mass (Witter & Cuthill 1993). A bird's mass should therefore increase as starvation risk increases, but might either increase or decrease as predation risk increases, dependent on the quality of the foraging environment in which it lives. In favourable environments, small birds may respond to increased predation risk by avoiding foraging at times and in places of higher predation risk, but because foraging opportunities become more constrained and so starvation risk increases as a result, individuals need increased energy reserves (the interrupted foraging or IF response; Houston & McNamara 1993; Lilliendahl 1998; Pravosudov & Grubb 1998; McNamara *et al.* 2005). For example, if a bird seeks to avoid foraging in times or in places because of a high-risk of encountering a predator it can only do so under certain circumstances. The environment must be sufficiently good for it to be able to meet its foraging requirements from a more limited set of safer foraging options. The bird also then needs to increase its fat reserves, which provides some insurance for the increased uncertainty that the shorter foraging time entails. In poor environments, however, individuals may have no choice but to continue to feed at

times and in places of higher predation risk. In this case, individuals can respond by reducing body mass (but at the cost of decreased reserves) so managing their predation risk by reducing their foraging exposure time and/or increasing their flight performance and chance of escape when attacked (the mass-dependent predation risk or MDPR response; Gosler *et al.* 1995; Kullberg *et al.* 1996; MacLeod *et al.* 2005a).

A consequence of a bird's mass change to increased predation risk being dependent on the quality of their foraging environment is that this mass change may then give us an index of the relative demographics of bird populations that differ in their mass response. Although many different factors influence population change, a large proportion are likely to exert their impact on populations through their effect on how individual starvation and predation risk affects survival (Sutherland 1996). In this study, we therefore develop and explore the hypothesis that mass change in response to predation risk can provide an index of whether populations are declining in birds, because mass change provides an indication of the foraging quality of the environment and therefore survival rates.

We suggest that an IF response, where birds offset any increased starvation risk resulting from restricting foraging opportunities to times of lower predation risk, should always be shown if foraging conditions allow because predation risk is minimized without increasing starvation risk. Birds that show the MDPR response, however, reduce their fat reserves, and so will face increased starvation risk because they can survive poor foraging conditions for a shorter time. The MDPR response should, we predict, only be shown by birds when the foraging environment is too poor to allow the individuals to meet their energy requirements during the reduced foraging opportunities that the IF response would require. Therefore, if individuals show an IF response to higher predation risk, we propose they are likely to be experiencing a high quality foraging environment that should lead to higher survival, and increased likelihood of stable or increasing populations. Whereas, individuals that show a MDPR response are likely to be in lower quality foraging environments, leading to relatively lower survival and this in turn is likely to increase the chance of population decline. We therefore predict generally that mass gain or loss in response to predation risk will correlate with population status because it provides an index of the general quality of the foraging environment that a population experiences.

We test the specific prediction that mass response to predation and starvation risk should reflect population status by relating mass and how it varied in response to increased predation risk (sparrowhawk *Accipiter nisus* Linnaeus abundance) and increased starvation risk (over the winter period) to species population status data for the 30 most commonly caught wintering passerine bird species in

Britain. We used predator density (sparrowhawk abundance) as our measure of predation risk because animals respond to increased abundance of predators by increasingly adopting more anti-predation behaviours (Lima & Dill 1990; Lima 1998a,b) Theoretically, increased predator density decreases prey fitness because of the starvation-predation risk trade-off, where increasing anti-predation behaviours, independent of the ratio of predators to prey, result in increased risk of starvation (Abrams 1993).

Firstly, we investigate the relationship between mass gain or loss in response to predation risk and population status across species while considering whether foraging habitat, guild, sociality, or size confounded any relationships. Secondly, we investigate mass response to predation risk within species; which allows us to consider the possibility that any link between mass response and population status between species might be due to mass response being a fixed species characteristic correlated with survival, rather than a flexible trait resulting from individual behaviour.

METHODS

The birds in the study were ringed between 1996 and 2004 as part of the British and Irish Ringing Scheme, organized by the BTO (Clark 2004). Species selection was determined entirely by the quantity of available data: we simply included all species of passerine in the BTO ringing database which had > 4000 computerized records ($N = 30$ species). The study focused on mass variation outside the breeding season so that body mass would not be influenced by changes due to reproduction. To effectively exclude the majority of early breeders, or the possibility of any migrants fuelling to leave the UK, this meant we used only capture records between October and January (Wernham *et al.* 2002). After removal of individuals not captured during this period and any records with missing data, overall sample size was $N = 333\ 879$ individuals and some species had only a few hundred records available for analysis (see Table 1).

For each first capture of an individual, ring number, date, time, & location of capture, were recorded and standard measurements of wing length to 1 mm and mass to 1 g were made (Redfern & Clark 2001). Daily rainfall, maximum air temperature, minimum air temperature, sunrise time, sunset time, day length and time as dawn for each capture where 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 data set of mass measurements from thousands of different individual birds (each sampled only once) allowed us to identify factors that determined mass variation across individuals, within and between populations, controlling for important confounding variables that also affect

Table 1 Species population status and mass responses

No.	Species	Scientific name[*]	LT	MT	C	HP	HS	HPHS	N	FH	FG	S
1	Meadow Pipit	*Anthus pratensis*	−32	0	1	**−0.15**	**1.73**	*0.35*	3474	O	G	1
2	Pied Wagtail	*Motacilla alba*	58	21	0	**+0.40**	**1.00**	**−0.34**	3186	O	G	1
3	Wren	*Troglodytes troglodytes*	68	14	0	**+0.10**	**0.14**	0.03	7098	C	GT	0
4	Dunnock	*Prunella modularis*	−29	13	1	+0.03	**0.83**	*−0.14*	8044	C	GT	0
5	Robin	*Erithacus rubecula*	45	15	0	**+0.53**	**2.04**	**−0.42**	13 961	C	GT	0
6	Blackbird	*Turdus merula*	−17	17	0	**+1.73**	**6.95**	**−0.88**	38 068	OC	GT	1
7	Fieldfare	*Turdus pilaris*	NA	NA	0	**+1.91**	**2.87**	0.88	3168	OC	GT	1
8	Song Thrush	*Turdus philomelos*	−50	14	2	**+1.51**	**4.32**	**−1.57**	8108	OC	GT	0
9	Redwing	*Turdus iliacus*	NA	NA	0	**+1.18**	0.30	0.31	8192	OC	GT	1
10	Blackcap	*Sylvia atricapilla*	124	54	0	**+0.21**	**0.96**	0.42	7589	C	T	0
11	Goldcrest	*Regulus regulus*	−9	60	1	**−0.04**	**−0.07**	0.05	20 390	C	T	1
12	Long-tailed Tit	*Aegithalos caudatus*	57	12	0	+0.01	**0.16**	*−0.04*	9211	C	T	1
13	Coal Tit	*Parus ater*	46	14	0	**+0.05**	**0.14**	**−0.06**	7590	C	GT	1
14	Blue Tit	*Parus caeruleus*	28	17	0	**+0.02**	**0.08**	**−0.05**	48 929	C	GT	1
15	Great Tit	*Parus major*	63	35	0	*±0.04*	−0.06	**−0.13**	20 454	C	GT	1
16	Treecreeper	*Certhia familiaris*	−5	7	0	+0.00	0.12	0.00	842	C	T	1
17	Starling	*Sturnus vulgaris*	−71	−30	2	−0.23	**2.31**	**−0.87**	7054	O	G	1
18	House Sparrow	*Passer domesticus*	−64	−3	2	**−0.54**	−0.01	*0.25*	5378	OC	G	1
19	Tree Sparrow	*Passer montanus*	−93	48	2	−0.14	−0.05	**0.37**	1728	OC	G	1
20	Chaffinch	*Fringilla coelebs*	32	9	0	**+0.18**	**0.63**	**−0.13**	27 108	OC	GT	1
21	Brambling	*Fringilla montifringilla*	NA	NA	0	**+0.20**	**0.51**	**0.65**	2743	OC	GT	1
22	Greenfinch	*Carduelis chloris*	26	37	0	**−0.05**	**0.42**	**0.11**	46 807	OC	GT	1
23	Goldfinch	*Carduelis carduelis*	49	28	0	**−0.10**	**0.20**	−0.01	8217	OC	GT	1
24	Siskin	*Carduelis spinus*	NA	−40	0	**+0.16**	**0.74**	−0.06	4203	OC	T	1
25	Linnet	*Carduelis cannabina*	−48	−14	2	**−0.59**	−0.05	0.04	2508	O	G	1
26	Twite	*Carduelis flavirostris*	NA	NA	0	+0.11	**0.34**	−0.05	2204	O	G	1
27	Lesser Redpoll	*Carduelis cabaret*	−90	−21	1	**−0.12**	−0.12	0.02	4132	OC	T	1
28	Bullfinch	*Pyrrhula pyrrhula*	−51	−9	2	−0.13	**0.65**	**−0.22**	2677	OC	GT	0
29	Yellowhammer	*Emberiza citrinella*	−54	−22	2	+0.07	**0.40**	0.09	2821	O	G	1
30	Reed Bunting	*Emberiza schoeniclus*	−43	4	2	**+0.14**	**0.63**	**−0.34**	7995	OC	G	1

LT and MT, population change 1970–2003 and 1994–2004 (%), respectively, C, conservation status (2 = Red, 1 = Amber, 0 = Green List). HP, mass response to higher predation risk (sparrowhawk abundance), HS, mass response to higher starvation risk period (winter compared with late autumn), HPHS, mass response to higher starvation and higher predation risk. The mass response parameter estimates are from general linear models for each species, parameters in bold are significant at $P < 0.01$, and italics at $P < 0.05$. N = sample size (no. individual birds) of GLM. FH, foraging habitat classification (O, open; OC, open and cover; C, cover). FG, foraging guild classification (G, ground; GT, ground and tree; T, tree). S, flocking behaviour (1 forms winter flocks, 0 does not form winter flocks). See MacLeod *et al.* (2005a) for a full account of an individual species model (blackbird) and effects of confounding variables.
*For authorities for all species names please see Dickinson (2003).

starvation risk and therefore mass, such as low temperatures and short daylength midwinter (Cresswell 1998).

For the individual species analyses, general linear modelling was used to investigate the effects of higher or lower predation risk, and periods of increased starvation risk, and their combination, on body mass in each species. Possible confounding effects of year (factor) and body size, minimum and maximum temperature, rainfall, day length and time of day (covariates), were controlled for by including these variables in each model when estimating the effect of starvation and predation risk (Cresswell 1998; MacLeod *et al.* 2005a). We controlled for spatial autocorrelation by including longitude and latitude of capture in all

models. We checked for non-linear effects of spatial autocorrelation by running all individual species models including latitude, latitude squared, longitude, longitude squared and longitude × latitude (see Kuhn 2007 for a similar example) and found that in no case (i.e. $n = 30$ individual species models) was the hawk parameter estimate 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 models as the most parsimonious approach to incorporating spatial data. The general modelling approach is in any case probably not confounded greatly by spatial autocorrelation because

removal of latitude and longitude from the individual species' models only resulted in the hawk parameter changing significantly in two of 30 species (one significant to non-significant, and another species the reverse): most of the variation in the data due to space was probably already captured by the environmental variables such as temperature and daylength (see Diniz-Filho *et al.* 2003 for a justification).

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 the ratio of predator to prey density (Lima 1986; Lima & Dill 1990; Abrams 1993; Houston *et al.* 1993). Sparrowhawks are the main avian predator of birds in Britain (Newton 1986) and their abundance has been shown to affect body mass of passerine birds (Gosler *et al.* 1995) so we used sparrowhawk breeding abundance data for $10 \times 10 \text{ km}^2$ of Britain (Gibbons *et al.* 1993) as a measure of the predation risk environment in the area of capture. 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. These are the best available data, but we believe that the temporal mismatch does not do more than increase the possibility of a type II error in our analysis (see Discussion). It is, however, likely that the breeding data is a reasonable representation of sparrowhawk status at the time of the study because sparrowhawks have (after a decline due to pesticide pollution) had a stable distribution in the UK since reaching their population and distribution maximum in the mid-1980s (Snow & Perrins 1998). 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). We classed the 50% of squares with above average number of sparrowhawks as higher perceived predation risk and the 50% of squares with below average number of sparrowhawks as lower perceived predation risk because there were many sampling points where low sparrowhawk density is recorded as zero (because the species was not always detected during survey where it is known to be present in small numbers), and because the measure of density is an index. Because of higher energy requirements and lower food predictability, average starvation risk will be higher in winter than in the autumn non-breeding period (Lima 1986). We used capture data from 4 months and classed the short, cold days of December and January as the higher starvation risk period and the warmer, longer non-breeding period days of October and November as lower starvation risk.

The GLM for each species gave a 'Hawk' parameter estimate that reflected how mass differed between lower and higher predation risk environments, a 'Starvation' parameter estimate that reflected how mass differed in respect of lower and higher starvation risk, and a 'Hawk × Starvation' interaction parameter estimate that reflected how mass differed when there was a combination of higher predation and higher starvation risk. Negative parameters signified that mass was reduced in the higher risk environment. General Linear Models were then carried out to test the relationship between species population status and mass change in response to predation risk and starvation risk. Population status, measured by percentage population change was the dependent variable. We used measures of population status in Britain as published by the BTO, where rates of change are modelled from yearly indices of population size (Baillie *et al.* 2005). We tested three measures: medium-term population change (1994–2004), which best fitted our mass data in term, but because of the relatively short time span gave less accurate estimates of population change; long-term population change (1970–2003), which gave more accurate estimates of population change because of the longer time period; and conservation status, whether a species was on the UK Red or Amber List of species of conservation concern. The species parameter estimates for the response to higher starvation risk (winter compared with late autumn), higher predation risk (higher sparrowhawk abundance) and combined higher starvation and predation risk were the independent variables. To ensure size differences between species did not bias the results, the parameter estimates were divided by mean non-breeding mass for that species before being used in the analysis. This allows a meaningful comparison between, for example, a 1-g mass increase in a 6-g bird such as a gold crest, and a 1-g mass increase in a 100-g bird such as a blackbird. Parameter estimates were not corrected for body mass for the intra-specific analysis.

We tested the effects of several potential confounding variables on the relationship between population change and the parameter estimates representing response to higher starvation risk, higher predation risk and combined higher starvation and predation risk, by using the information theoretic approach (Burnham & Anderson 2002). We use this model selection approach because we have a small sample size at the species level and so models with even a few independent variables will have limited power, therefore, an unbiased method of determining minimum models is necessary (Whittingham *et al.* 2006). We considered the following additional variables might confound the results of our main models: foraging habitat, foraging guild, sociality and size (e.g. see Rogers 1987). Species were classified into one of three foraging habitat types: open (e.g. Meadow Pipit); open and cover (e.g. Blackbird); and cover (e.g. Blue Tit). Species were classified into one of three foraging guilds: ground (e.g. Pied Wagtail); ground and tree (e.g. Great Tit);

tree (e.g. Treecreeper). Species were classified into one of two sociality classes: flocking (e.g. Yellowhammer), solitary (e.g. Wren). Species' size was estimated by using mean wing length (from our capture data set). Data to make these classifications were taken from regional handbooks, e.g. (Cramp 1988) and the full classification is shown in Table 1.

All possible models (255) incorporating the seven independent variables (the four above and our three predation and starvation risk response parameters), and a random variable (random values generated using SPSS with the same mean and variance as the response to predation risk parameters) were run using the GenMod procedure in SAS version 9.1 (SAS Institute Inc., Cary, NC, USA). Akaike's information criterion was calculated from AIC_c (because of small sample size) for each model (Hurvich & Tsai 1989). The models were then ranked according to AIC weight and the 95% confidence limit set of models was established. The sum of Akaike weights for each variable were then calculated across the 95% confidence limits set of models [effectively allowing the variables to be ranked according to their predictive power, with the random variable setting the lower limit below which variables could be considered not to be predictors – see (Whittingham et al. 2005)]. To obtain confidence limits for our random variable we then ran this procedure 25 times, each with a different set of values for the random variable. The significance of a variable as a predictor to be included in the final model was then determined by matched pairs t-tests of each variable against the random variable ($N = 25$); if the variable had a significantly higher summed Akaike weight than the random variable, then it was included in the final model.

For the within species analyses, individuals were classed into two groups based on whether population change in region of capture was below or above the average change for that species, using BTO data for population change (Raven et al. 2005) in the nine English government regions and Scotland & Wales. For the 24 species with regional population change data (Table 2) we reran the original individual species GLMs for the two population change groups and examined the parameter estimates for mass response to higher predation risk.

RESULTS

Across species relationships

In response to higher predation risk, seven species showed a significant decrease in mass probably because of a mass-dependent predation risk response, and 14 species showed a significant increase in mass, probably because of an interrupted foraging response (Table 1). Across the 25 bird species for which we had published population data (Table 1) there was a highly significant positive relationship between mass change in response to higher predation risk and population change between 1970 and 2003 (model 1: $F_{1,21} = 9.1$, $P = 0.007$, $R^2 = 0.33$, Table 2a). For the species in Fig. 1, those that reduced mass in response to higher predation risk tended to show population decline (mean population change $-38.3 \pm 15.0\%$, $N = 10$), while those that increased mass in response to higher predation risk tended to show population increase (mean population change $21.5 \pm 13.5\%$, $N = 15$). This difference in population change was highly significant (59.8%, $t_{23} = 2.9$, $P = 0.008$).

Similar results were obtained when population change from 1994 to 2004 was examined (see Table 1), with mass response to higher predation risk significantly correlating with population change (Table 2, model 2: $F_{1,22} = 7.5$,

Table 2 General Linear Models showing a significant relationship between species population status and mass strategy in response to predation risk but not starvation risk

Source of Variation	Sum of Squares	d.f.	F	Sig.	Parameter estimate
(a) Model 1					
Starvation	2316	1	0.9	0.352	-401.2 ± 421.9
Hawk	23 232	1	9.1	0.007	3574.2 ± 1186.9
Starvation & Hawk	67 612	1	2.6	0.119	1688.7 ± 1039.4
Explained	25 986	3	3.4	0.037	
Error	53 794	21			
Total	79 780	24			
(b) Model 2					
Starvation	1531	1	3.2	0.087	-324.0 ± 180.6
Hawk	3548	1	7.5	0.012	1392.6 ± 509.8
Starvation & Hawk	3026	1	6.4	0.019	1127 ± 447.1
Explained	4721	3	3.3	0.039	
Error	10 463	22			
Total	15 185	25			

(a) Population change 1970–2003 ($R^2 = 0.33$, adjusted $R^2 = 0.23$). (b) Population change 1994–2004 ($R^2 = 0.31$, adjusted $R^2 = 0.22$).
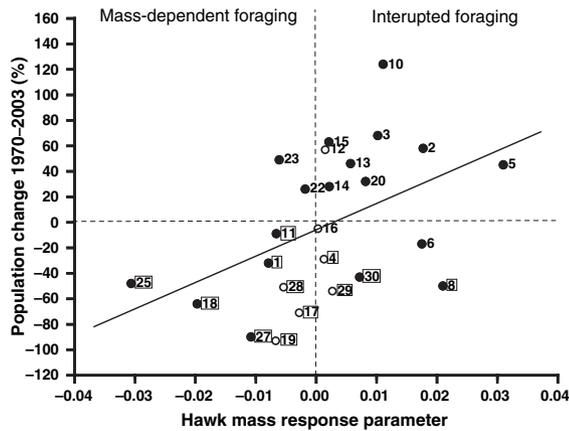
Figure 1 Relationship between mass response to higher sparrow-hawk abundance and population change for 25 common British bird species. Species are: 1 *Meadow Pipit*, 2 Pied Wagtail, 3 Wren, 4 Dunnock, 5 Robin, 6 Blackbird, 8 Song Thrush, 10 Blackcap, 11 *Goldcrest*, 12 Long-tailed Tit, 13 Coal Tit, 14 Blue Tit, 15 *Great Tit*, 16 Treecreeper, 17 *Starling*, 18 *House Sparrow*, 19 *Tree Sparrow*, 20 Chaffinch, 22 *Greenfinch*, 23 Goldfinch, 25 *Linnet*, 27 *Redpoll*, 28 Bullfinch, 29 Yellowhammer, 30 Reed Bunting. Species in italics were classified as mass-dependent predation species (lost mass), and the rest interrupted foraging species (gained mass): a filled circle indicates a significant mass response parameter; a species label enclosed in a box indicates a species of conservation concern (on the UK Red or Amber list).

$P = 0.012$, $R^2 = 0.31$). This model also showed that while the mass response of a species to higher starvation risk was, as before, not significantly linked to population change, the response to combined higher starvation and predation risk

was significantly correlated with population change (Table 2, model 2: $F_{1,22} = 6.3$, $P = 0.019$).

Further analysis using the information theoretic approach (Burnham & Anderson 2002) testing the confounding effects of foraging guild, foraging habitat, sociality index and size showed that mass response to higher predation risk was the most significant predictor for population change 1970–2003 and that the response to combined higher starvation and predation risk was the most significant predictor for population change 1994–2004 (Tables 3 and 4). This analysis also confirmed that species in open habitats (mainly farmland species) were significantly more likely to have declining populations (Table 4).

Mass response to predation risk was also significantly correlated with a species' conservation status: the 12 UK Amber and Red List species of conservation concern (Table 1) showed on average a negative mass response to higher predation risk (mean hawk response parameter -0.005 ± 0.005) while the 18 other species not of special conservation concern increased mass on average (mean hawk response parameter 0.009 ± 0.002) and these responses were significantly different ($t_{28} = 3.5$, $P = 0.002$).

Within species relationships

If mass response were a fixed species characteristic we would predict no within species changes in the mass response to higher predation risk. In contrast, our hypothesis predicts that the mass response is a behavioural trade-off by individuals, so we should see within species changes in mass response and these should be connected to population status. Contrary to the idea that mass response

Table 3 The sum of Akaike weights for the 95% confidence set of all possible models including the three variables of biological interest, four potential confounding variables and a random variable

	Dependent variable: population change during					
	1970–2003			1994–2004		
	Sum of Akaike weights for 95% confidence model set					
Independent variable	Mean	SE	Sig.	Mean	SE	Sig.
Starvation	0.189	0.004		0.253	0.002	
Hawk	**0.765**	0.009	< 0.001	**0.388**	0.003	< 0.001
Starvation & Hawk	0.266	0.002		**0.625**	0.004	< 0.001
Wing length	**0.477**	0.007	< 0.001	0.234	0.001	
Foraging habitat	**0.438**	0.015	< 0.001	**0.516**	0.006	< 0.001
Foraging guild	0.115	0.001		0.111	0.002	
Sociality	0.158	0.001		0.170	0.0004	
Random numbers	0.233	0.029		0.228	0.015	

The random variable is included to determine the level at which an Akaike weight indicates a significant predictor. Sums were calculated 25 times with a different set of random variables each time to generate confidence intervals. The significance of any variable having an Akaike weight above that of the random variable was then tested with matched pairs *t*-tests ($N = 25$) for all variables against the random variable weight.

Table 4 General Linear Models showing the relationships between species population status and the variables identified as being significant predictors during the information theoretic analysis

Source of variation	Sum of squares	df	F	Sig.	Parameter estimate
(a) Model 1					
Hawk	12 013	1	5.4	0.030	2092.6 ± 897.0
Wing length	3720	1	1.7	0.208	−0.85 ± 0.66
Foraging habitat	1411	1	0.6	0.433	14.7 ± 18.4
Explained	33 434	3	5.0	0.009	
	46 346	21			
	79 780	24			
(b) Model 2					
Hawk	687	1	1.6	0.217	514.1 ± 404.1
Starvation & Hawk	2007	1	4.7	0.041	928.3 ± 426.9
Foraging habitat	2657	1	6.3	0.020	14.5 ± 5.8
Explained	5847	3	4.6	0.012	
	9337	22			
	15 185	25			

(a) Population change 1970–2003 ($R^2 = 0.42$, adjusted $R^2 = 0.34$).
(b) Population change 1994–2004 ($R^2 = 0.39$, adjusted $R^2 = 0.30$).

might be a fixed species characteristic, 63% of species had significantly different mass response parameters comparing groups of above and below average population change (Fig. 2). 38% species actually switched their direction of mass response strategy from gain to loss (i.e. from interrupted foraging to mass-dependent response), or vice versa, dependent on their population status (Fig. 2).

To further investigate the link between mass response and predation risk, we examined individual species' responses in two groups, those showing a MDPR and an IF response based on Table 1. For the MDPR response species, we expected mass loss to be closely associated with degree of population decline because starvation risk will be increased as energy reserves, and body mass, are reduced (Lima 1986; Rogers & Smith 1993). As expected individuals in populations that showed below average population change showed a greater decrease in mass in response to higher predation risk (paired sample t-test, mean difference: 0.16 ± 0.06, $t_7 = 2.8$, $P = 0.028$, $N = 8$ within species pairs: Fig. 2a). For the IF response species, the degree of population increase is likely to be associated with the degree of mass gain but less strongly. Although better environmental conditions will allow the individual to interrupt its foraging more, these conditions should also allow the individual to adopt a wider range of alternative antipredation behaviours (e.g. more time allocated to vigilance etc), which may allow less mass to be gained (Lind & Cresswell 2005). In line with this expectation, we found that for the interrupted foraging group, there were differences in mass response for individuals in populations of below and
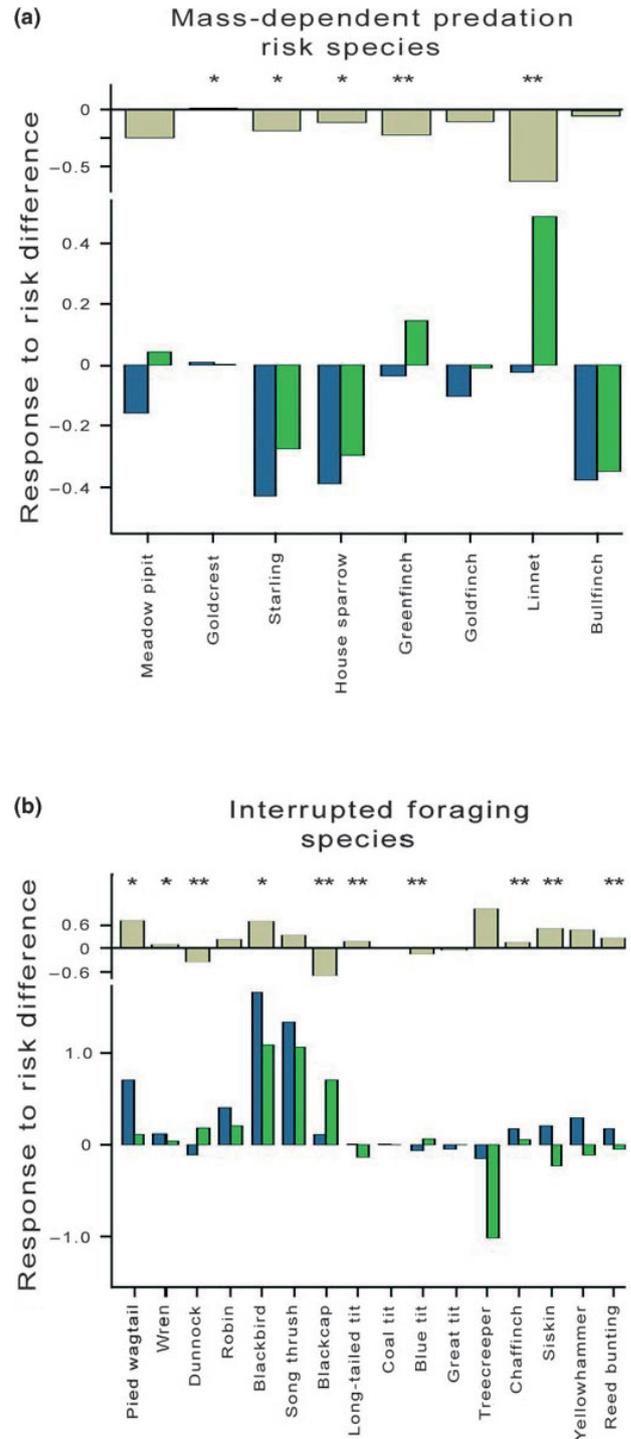

Figure 2 Different within species mass change to due to higher predation risk (higher sparrowhawk abundance) in areas of below (blue) and above (green) average population change: the difference (above minus below) is shown in grey. *Significant differences in mass response at $P < 0.05$ and **$P < 0.01$, i.e. the results for the population change area × predation risk interaction added to original individual species GLMs.

above average change but these difference were variable (Fig. 2b) and overall with the available sample size the relationship was non-significant (paired sample *t*-test, mean difference 0.18 ± 0.09, t_{15} = 2.0, P = 0.066, N = 16 within species pairs: Fig. 2b). Thus, although the IF response of mass gain is associated with population growth the greater potential variability of predation response appears to make it harder to use the mass response to predict the size of population growth of an IF species.

DISCUSSION

Our results show that mass response to predation risk in birds may be able to predict population status and support the hypothesis that this is because mass provides an index of the quality of the foraging environment. But, despite the unique and large data set our results are only correlative, nevertheless they do clearly suggest that birds regulate their mass as a response to both interrupted foraging and mass-dependent predation risk, and suggests a clear hypothesis to link environmental quality to population dynamics.

Our results are likely to be robust because we have used data of relatively low resolution, which will tend to make our tests conservative. For example, the population decline data has large confidence limits (Baillie *et al.* 2005) and is missing for several species. Population declines in species vulnerable to a poor foraging environment are more likely to be picked up and the patterns of decline will become clearer with increasing numbers of years of data, so that recent decline data (i.e. the short term decline data 1994–2004) is likely to be less accurate in detecting declines than the longer term dataset (i.e. 1970–2003 in many cases). There is a similar situation with the resolution for the sparrowhawk abundance data that spans 1988–1991. 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 which 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 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.

Another limitation of our analysis is that we use only a small range of species. This means the statistical power available to test any number of potentially confounding variables simultaneously is limited. A variable we identified as important but which did not actually confound the results was habitat: habitat is probably important because it could interact with sparrowhawk population size to determine predation risk, particularly with farmland birds (Evans 2004). Open habitat species may not have any refuges available to avoid predators and so may be more likely to be

forced to adopt MDPR responses, this then makes these species even more vulnerable to fluctuations in the quality of the foraging environment because they carry reduced fat reserves (Lind 2004).

One apparently important potential confounding variable that we did not consider because suitable data were not available – variation in species' density – should probably be discussed in more detail. Intuitively, it seems that if a prey has a high population and therefore density, then predation risk will be diluted (Foster & Treherne 1981). Species with a high density might then have a lower mass response to any given level of hawk abundance. If prey density was simply a confounding variable, where mass responses to hawks are weaker in areas where predation risk is diluted by high-prey species density, this would simply strengthen our results as they occur despite an increased chance of a Type II error. In reality, however, theoretical and empirical evidence suggests that behavioural and physiological compensation to predation risk is not dependent on prey density but is rather dependent on an individual's perceived risk of predation, which unlike overall proportion of predation mortality in the population is largely dependent on local predator density rather than prey density (Lima 1986; Lima & Dill 1990; Houston *et al.* 1993).

The results and hypothesis we present here build on the field and experimental work carried out on the great tit *Parus major,* the best studied species in this context. Great tits have been shown in the past to show a MDPR response to sparrowhawks in the wild, both historically (Gosler *et al.* 1995) and experimentally (Gentle & Gosler 2001; MacLeod *et al.* 2005b), and to show an IF response after a single short capture by humans (MacLeod & Gosler 2006). Our results now show the national great tit population (between 1996 and 2004) adopting on average a small IF response (Table 1) close to the transition between the IF and MDPR responses (Fig. 1). In contrast, our within species analysis (Fig. 2) shows the species adopting a small MDPR response when experiencing below average population change. These results confirm that mass response is a flexible behaviour and all are consistent with our hypothesis that mass is indicative of an individual's behavioural response to the quality of the environment with an MDPR response occurring in poorer environments and IF when conditions are more favourable. The change from great tits on average being historically a MDPR species to a current IF species suggests that environmental conditions may have improved on average for great tits, as has been shown for some populations (Cresswell & McCleery 2003).

General implications

Our results have general implications for the experimental study of mass change in birds. Theoretical models predict

that an increased risk of predation will result in a lowering of body mass in birds (Lima 1986; McNamara & Houston 1987; Houston & McNamara 1993) and many experimental and field studies have shown this to be the case (Gosler *et al.* 1995; Lilliendahl 1997; Carrascal & Polo 1999; van der Veen & Sivars 2000). However, a number of studies have shown the opposite effect, with birds increasing in mass in response to increased predation risk, e.g. (Fransson & Weber 1997; Lilliendahl 1998; Pravosudov & Grubb 1998) because the presence of the predator creates interruptions in foraging and thus increased the perceived starvation risk (Lima 1986). Our results provide strong support for the interrupted foraging hypothesis, showing that mass gain may be a general and likely response to increased predation risk in probably most passerine species, at least when their foraging environment is sufficiently good so the individual bird can meet its daily energy demands within the reduced time available for foraging. Our results suggest that it is the quality of the foraging environment (e.g. predictability and availability of foraging opportunities) that determines whether mass is gained or lost by a bird with increased predation risk: thus experiments, which simply alter predation risk without considering the foraging environment cannot reliably predict whether mass will be lost or gained.

Our results add general support to the idea that trait mediated interactions or non-lethal effects are crucial in structuring population dynamics and community effects (Werner & Peacor 2003) and that the starvation-predation risk trade-off provides a framework in which to model the strength of predation risk and its consequences for population dynamics (Abrams 1984, 1993; McNamara & Houston 1987). For example, foraging-predation risk trade-off functions can be used successfully to explain diverse ecosystem processes (Bolker *et al.* 2003). In essence, our results provide further evidence that predation is best appreciated as a foraging cost, and foraging theory can be used to measure it quantitatively or qualitatively, as well as how animals perceive predation risk (Brown 1999; Brown & Kotler 2004).

Our results also have interesting implications for environmental monitoring. Our approach could potentially be applied to predicting population status or testing hypotheses about declines in specific areas or in species with only limited data. Identifying, which species are declining is crucial to conservation management, but monitoring population change often requires costly data collected over a long period of time e.g. (Krebs *et al.* 1999; Dunn 2002; Hole *et al.* 2002; Maxwell & Jennings 2005). Although our results used very large data sets, previous experiments on wild birds have shown that mass responses to the starvation-predation risk trade-off can easily be monitored with repeated weighing of tens of individuals (Cresswell 1998). Perhaps

most significantly, our results suggest that historical data sets of mass (which has been routinely collected during bird ringing for the last century) could be used to investigate the factors that influenced unmonitored population declines.

Our results, however, show that mass response to predation risk in birds can predict conservation status only to a degree and we therefore present them as evidence supporting a working hypothesis that will need further investigation to develop. Our analysis, although significant, only successfully predicted eight of 12 species of conservation concern correctly. Clearly, other factors can also be important and studying mass response should help indicate when these other factors may be more important than the foraging environment. For example, where species show interrupted foraging, but also show a population decline (e.g. song thrush and blackbird in Fig. 1), then this suggests that factors other than over winter survival may be the predominant cause of any population decline. Mass response may therefore only reliably provide an indication of population decline across a range of species (i.e. on average) and so may be more suitable to identifying areas where environmental quality is poor or declining. For example if a species, or range of species show a mass loss in area A, and a gain in area B (when predation risk differences are controlled for) then it would be reasonable to conclude that area A is of lower foraging quality than Area B. This study may then provide the first evidence of how mass in birds may provide a powerful, quick and cheap tool for identifying areas or habitats where populations might be at future risk of decline due to environmental change.

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