

Do great tits (*Parus major*) suppress basal metabolic rate in response to increased perceived predation danger? A field experiment



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HIGHLIGHTS

- Higher metabolic rates (MRs) are sometimes associated with higher feeding rates
- Thus, high MRs may expose animals to more predation risk
- We tested whether MR is adaptively suppressed under elevated predation danger
- Great tits suppressed seasonal increases in MR in treatment but not control plots
- The magnitude of the effect was small (approximately 1%)

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ABSTRACT

Several studies have shown that individuals with higher metabolic rates (MRs) feed at higher rates and are more willing to forage in the presence of predators. This increases the acquisition of resources, which in turn, may help to sustain a higher MR. Elevated predation danger may be expected to result in reduced MRs, either as a means of allowing for reduced feeding and risk-taking, or as a consequence of adaptively reducing intake rates via reduced feeding and/or risk-taking. We tested this prediction in free-living great tits (*Parus major*) using a playback experiment to manipulate perceived predation danger. There was evidence that changes in body mass and BMR differed as a function of treatment. In predator treatment plots, great tits tended to reduce their body mass, a commonly observed response in birds to increased predation danger. In contrast, birds from control treatment plots showed no overall changes in body mass. There was also evidence that great tits from control treatment plots increased their basal metabolic rate (BMR) over the course of the experiment, presumably due to decreasing ambient temperatures over the study period. However, there was no evidence for changes in BMR for birds from predator treatment plots. Although the directions of these results are consistent with the predicted directions of effects, the effects sizes and confidence intervals yield inconclusive support for the hypothesis that great tits would adaptively suppress BMR in response to increased perceived predation risk. The effect size observed in the present study was small (~1%) and would not be expected to result in substantive reductions in feeding rate and/or risk-taking. Whether or not ecological conditions that generate greater energetic stress (e.g. lower food availability, lower ambient temperatures) could produce an effect that produces biologically meaningful reductions in feeding activity and/or risk-taking remains an open question.

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1. Introduction

Among-individual differences in resting or basal metabolic rates (MRs) have recently received increasing attention as potentially important correlates of among-individual differences in behaviour [1–3]. In some cases, higher MRs may favour higher expression of behaviours associated with resource acquisition [4,5]. At the same time, a higher expression of such behaviours may facilitate the maintenance of costly

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metabolic machinery [3 and references therein, 6]. Indeed, several studies have found that individuals with higher MRs spend more time foraging [4,7], behave more boldly in the face of predators [8–11] or are more constrained in their behavioural responses to predation danger [4].

All else being equal, higher feeding rates and greater risk-taking expose individuals to a higher risk of mortality due to predation, and consequently, individuals with lower MRs may be expected to have an advantage under conditions of high predation danger. Indeed, mealworm beetles (*Tenebrio molitor*) with higher MRs suffer higher mortality due to predation [8,9]. Suppression of feeding rates and risk-taking behaviours are well documented in animals under conditions of elevated predation danger [12]. Such suppression of feeding rates is considered adaptive because it reduces immediate exposure to predators. However, numerous studies have shown that long-term reductions in feeding rate can also lead to reductions in MR [reviewed in 13]. Thus, sustained reductions in feeding rate in response to long-term elevations in predation danger may also mitigate predation danger by favouring reduced MRs, which in turn may allow individuals to sustain lower intake rates and lower levels of risk-taking behaviours (Fig. 1).

Here, we report on an experiment that manipulated perceived predation danger in a free-living population of great tits (*Parus major*). The aim of our study was to test the prediction that increased predation danger leads to within-individual reductions in basal metabolic rate (BMR). Great tits are a good study system in which to test this prediction, because previous work in this population showed that higher BMR was associated with higher feeding rates and constrained behavioural responses to increased perceived predation danger [4]. This suggests that there should be a cost to high BMR under conditions of high predation danger. Furthermore, great tits are able to adjust their BMR to current ecological conditions [14, e.g. ambient temperature, 15] suggesting that within-individual changes in BMR in response to temporal variation in predation danger is physiologically possible. Finally, because great tits readily roost in artificial nest boxes, marked individuals can be recaptured with ease, facilitating the study of within-individual variation in free-living populations [16].

2. Materials and methods

2.1. Playback experiment

The experiment was carried out in 8 forest plots located in Bavaria, Germany (48°N, 11°E) in the winter of 2014 (Fig. 2) under Regierung von Oberbayern permit no. 55.2-1-54-2532-140-11. Each plot consists of 50 nest boxes hung in a regular grid, with 50 m between adjacent nest boxes. Perceived predation danger was manipulated at the plot

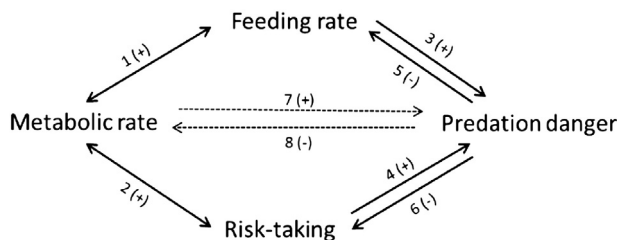


Fig. 1. Illustration of hypothesized relationships between MR, behaviour and predation danger. Direct (causal) relationships are illustrated with solid arrows, indirect relationships are illustrated with dotted arrows. The nature of the relationship (positive or negative) is indicated in parentheses. If higher MR requires greater total energy intake, it may favour higher feeding rates (1) and greater risk-taking (2). The greater resource acquisition conferred by these behaviours may in turn facilitate the maintenance of higher MRs (illustrated by doubled sided arrows in (1) and (2)). All else being equal, higher feeding rates (3) and greater risk-taking (4) expose animals to greater risk of predation, resulting in a positive indirect relationship between MR and predation danger (7). However, because higher predation danger favours adaptive suppression of feeding rate (5) and risk-taking (6), increasing predation danger may indirectly result in reduced MR (8).

level (4 predator plots and 4 control plots, see below). Assignment of treatment to plots was randomized, while ensuring that there were no initial differences between predator and control plots in roosting densities or body mass based on data from the previous winter. Treatments were also stratified with respect to perceived predation danger treatments that were performed the previous breeding season as part of a separate experiment [17, see Supplementary Table S1].

Perceived predation danger was manipulated using playbacks. In early January 2013, 4 speakers were placed in each plot such that there was good auditory coverage of the entire plot. Sound files used to experimentally increase perceived predation danger consisted of either Eurasian sparrowhawk (*Accipiter nisus*) calls (a natural predator of great tits) or great tit mobbing calls (typically produced in response to predator encounters). For the control playbacks we used common chaffinch (*Fringilla coelebs*) calls and Eurasian wren (*Troglodytes troglodytes*) songs. These control sounds were chosen because both species are common in the study area, call and sing regularly during the period of the experiments (January through February), and do not compete with the focal species. In total, 8 unique sound files were created for each sound type using recordings obtained from the Xeno-canto (www.xeno-canto.org/) bird song repository. Each sound file was 3 min long. Sound files of Eurasian wren songs and sparrowhawk calls were comprised of alternating bouts of sounds and silences of (5 to 15 s of sound followed by 5 to 15 s of silence, on repeat for 3 min), while chaffinch call and great tit mobbing call sound files were made up of continuous vocalisations (i.e. no prolonged bouts of silence). This was done to mimic the vocalisation patterns normally heard for each of these song and call types.

Playbacks were programmed so that 1 sound file played at each speaker within a plot per hour (4 different sound files per plot per hour) between dawn and dusk. The exact interval between subsequent playbacks was randomized. Sparrowhawk calls (or chaffinch songs for control plots) were limited to 2 per day per plot; 1 in the hour following sunrise and 1 in the hour preceding sunset. This was done to mimic the natural timing and frequency of sparrowhawk calls during the months of the experiment, and to minimize habituation effects. Due to technical difficulties with the speakers, playbacks did not commence until 2 weeks after the first roosting inspections, and were then carried out for 3 weeks in each plot.

2.2. Roosting inspections and BMR measurements

Immediately after speaker placement in early January, but before playbacks began, roosting inspections were performed after sunset in each of the plots following standard protocols [18]. During roosting inspections, all birds were marked with aluminum rings if not already marked and brought to the laboratory for behavioural and morphological measurements as part of the general data collection for this study population [details provided in 16] (January, $N = 143$; February, $N = 115$). Predator and control treatment plots were sampled alternately, to avoid confounding treatment and date. The roosting inspection of a given plot ended either when all 50 nestboxes had been checked, or when 24 roosting birds had been collected ($N = 6$ occasions of 16), as this was the maximum number of birds that could be held in the laboratory overnight. In these cases, the remaining nestboxes were checked the following evening. Our equipment allowed measuring BMR for up to 9 individuals per night. Thus, nine individuals were randomly selected from the total number of birds that were brought into the lab on any given night. In total, we measured BMR of 111 individuals during the pre-treatment period (January) and 65 individuals during the post-treatment period (February). Thus, we obtained a repeated measure (i.e., 1 pre- and 1 post-manipulation measurement) for a total of 56 individuals.

A detailed description of the respirometry setup is provided in the Electronic Supplementary Material (ESM text S1). Briefly, BMR was measured as O_2 consumption rates using three identical setups, each measuring up to 3 birds per night. Upon arrival in the laboratory

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