



Physiological responses to increased brood size and ectoparasite infestation: Adult great tits favour self-maintenance[☆]



Michele Wegmann^{*}, Beatrice Voegeli, Heinz Richner

Evolutionary Ecology Lab, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

HIGHLIGHTS

- We studied parental responses to two concurrent stressors.
- We measured different stress responses and physiological parameters.
- Adults favour maintenance of cellular homeostasis over current reproduction.
- Adults show moderate stress response in order to keep energy expenditure low.
- Costs of stressors are carried by the offspring and may have additive effects.

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ABSTRACT

Different types of stressors trigger responses of different physiological systems, and these responses may contribute differentially to the maintenance of homeostasis, to trade-offs and the evolution of life-history traits. To manipulate two common stressors during reproduction, we infested half of the nests in a naturally breeding great tit population with ectoparasites and simultaneously manipulated brood size, using a 2×2 experimental design. Parents in this model species commonly compensate for ectoparasites by an increase in food provisioning. We assessed parental responses to these concurrent stressors by measuring several physiological stress parameters such as changes in metabolic rate, oxidative stress and expression of heat-shock proteins (Hsp), and explored how these stressors affect the trade-off between self-maintenance and reproduction. Neither flea infestation nor brood size manipulation affected adult metabolic rate, oxidative damage or Hsp levels. Furthermore, we found no interactive effect of the two treatments on adults. However, nestlings in infested nests had lower body mass and lower survival. Nestlings in enlarged broods were lighter and had lower survival, although parents of enlarged broods increased food provisioning rate. The findings suggest that adults favour maintenance of cellular homeostasis, and physiological equilibrium over current reproduction, and that the costs induced by both stressors, flea infestation and increased brood size, are carried by the offspring. It emphasizes the importance of self-maintenance over reproduction in life-history decisions, and more generally the need of including physiological traits for understanding the evolution of life-histories.

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1. Introduction

Behavioural and physiological responses as an adaptation to the current environment [44] are important to understand ecology and life-histories [50,54]. The expression of life-history traits is regulated by physiological processes at different levels including the endocrine system, metabolic rate, immune response and oxidative balance [43, 50], which build interconnected networks of molecules to maintain homeostasis [13,31]. Stressful conditions are important ecological and

evolutionary forces triggering adaptive responses in natural populations [14,51]. A stressor is an unpredictable or uncontrollable environmental stimulus that threatens an organism's survival or homeostasis (for a review see [4] and references therein). Stress is metabolically expensive due to the molecular and cellular damage and their associated costs arising for example from the synthesis of stress proteins and the re-establishing of homeostasis [31]. Thus the question is how organisms regulate investment in self-maintenance versus investment in current offspring, especially under stressful conditions.

Different types of stressors trigger responses of different physiological systems and hence it is of interest to understand how these responses contribute to the maintenance of homeostasis [9,13]. The release of glucocorticosteroids is the most commonly assessed stress response in ecology and evolution, yet other metrics such as oxidative stress, stress

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^{*} Corresponding author.

E-mail address: michele.wegmann@gmail.com (M. Wegmann).

protein response and body mass changes may be equally important for the understanding of stress biology [6]. Oxidative stress, defined as an imbalance between pro-oxidants and antioxidants in favour of the former [55], may play an indirect role in inducing the cellular stress response [31,57]. Heat shock proteins (Hsp) are crucial for the maintenance of cell homeostasis, since they are part of the cellular stress response and involved in protein repair [22,36]. Furthermore, they are expressed throughout the whole animal kingdom and are increased in response to a range of stressors (e.g., radiation, heavy metal, parasitism, oxidative stress), and thus they play an important role in buffering environmental variation ([59] and references therein). They are activated in response to protein damage, caused by an increased production of reactive species (RS) during stress. Immunological studies revealed the relevance of Hsps and their role in the adaptive and the innate immune system [29,41,61,72].

Studies that integrate measures of metabolic rate, oxidative stress and heat-shock protein levels in response to stress and individual investment in reproduction are lacking. Studies that looked at these measures individually give insight into some of these aspects. Birds can raise more offspring than they actually planned, as demonstrated with brood size manipulation experiments for example in great and blue tits [45,53,65], albeit at the expense of survival and future reproduction. The increased workload results in elevated energy expenditure and increased food intake [42]. High metabolic rates generate RS with potentially detrimental effects [71] as shown in zebra finches, where birds with experimentally increased broods showed a reduction in antioxidant defence and a significant mass loss [1,73]. Increased energy expenditure can decrease future reproduction and survival as shown in kestrels, where parents of enlarged broods had significantly lower chance of survival to the next breeding season ([18]; but see review by [52]). In another study, heat-shock protein levels were measured in response to increased parental investment. Female blue tits raising reduced broods showed a significant decrease in the level of Hsp60, while Hsp levels in females of control or enlarged nests remained unchanged [38]. This reduction may imply that females are naturally working close to maximum levels of cellular stress, and a decrease only of the workload and the related metabolic activity may reduce the cellular stress response [38]. Thus the functional base for a cost of reproduction seems to be the detrimental effects of high metabolism rather than energy allocation between maintenance and work rate [42]. This is in contrast to a study performed in great tits, where males of enlarged broods with an associated 50% increase of food provisioning rates showed a doubling of hematozoan parasites [49]. This suggests a trade-off between investment in reproduction versus parasite defence [49], which was also shown in barn swallows infested with fowl mites [39]. In other studies, birds responded to infections directly with higher immunoglobulin levels [68], increased heat-shock protein levels [37], oxidative stress [62] and increased field metabolic rate [30], or indirectly by compensating for increased begging of nestlings with higher food provisioning [69].

Here, we tested the combined effects of increased workload and exposure to ectoparasites on various stress responses, and how these physiological responses affect the trade-off between investment in self-maintenance and reproduction. In a wild population of great tits (*Parus major*), we performed a 2×2 factorial design using manipulation of brood size (enlarged and control) and hen flea infestation (*Ceratophyllus gallinae*), assessed stress responses measured as Hsp levels, oxidative stress and field metabolic rate. We measured offspring body mass and nestling survival before fledging to assess investment in current reproduction.

Parents raising enlarged broods are predicted to show an increase in energy expenditure, oxidative stress, and heat-shock protein levels due to cell damage caused by reactive species. Parents of infested broods are predicted to show an increase in Hsp levels, oxidative stress, and energy expenditure following a predicted increase in food provisioning rates to compensate for infestation. Effect of brood size manipulation and

parasite treatment may be additive depending on the physiological trade-offs involved.

2. Material and methods

The experiment was carried out in a great tit (*P. major*) population in a forest near Bern, Switzerland (47°56' N, 7°18' E) in 2011. All nest-boxes were visited at least twice a week from mid March onwards to monitor nest-building activity and to determine the start of incubation. After 10 days of incubation, nests were visited daily to determine hatching date, defined as day 0. Parents were captured in their nest boxes with spring traps when nestlings were 11-days old. Adults and nestlings were ringed with individually numbered aluminium rings (Vogelwarte Sempach, Switzerland) and we measured body weight to the nearest 0.01 g, tarsus (± 0.1 mm) and wing length (± 0.5 mm). The measurements of the nestlings were taken on days 8 and 15 post-hatch. Age of adults was assessed based on the wing coverts [63], or if known from previous ringing information. Additionally, we took a blood sample (80 μ l maximum) from the wing vein to analyse antioxidant capacity and oxidative damage from plasma, and daily energy expenditure (DEE, see below).

2.1. Brood size manipulation and flea infestation

Brood size manipulation and flea infestation were combined in a 2×2 factorial design. Three days after hatching, whole broods were exchanged between broods having identical hatching date (± 1 day) and either the same number of chicks (control), two chicks more (enlarged) or two chicks less (reduced), and infested with fleas (enlarged with fleas $n = 38$ broods enlarged without fleas $n = 34$, control with fleas $n = 38$, control without fleas $n = 34$). The reduced group was excluded from the analysis since the focus of the study was on the physiological and homeostatic responses to an increase in reproductive stress factors. Whole broods were exchanged to maintain sibling hierarchy and genetic relatedness since both can influence patterns of interactions among offspring [35] and stress responses. Enlarged and control broods did not differ in original brood size ($F_{1,149} = 2.97$, $p = 0.09$). During cross-fostering, we heat-treated nests in a microwave appliance to eliminate nest-parasites [48] and randomly assigned each pair of cross-fostered broods to parasite-free nests, or nests infested with 100 hen fleas (*C. gallinae*). The hen fleas used for the infestation were obtained from old nest material of the same population. There was no significant difference in laying (brood size manipulation, $p = 0.66$; flea treatment, $p = 0.30$) and hatching date among experimental treatment groups (ANOVA: brood size manipulation, $p = 0.25$; flea treatment, $p = 0.53$).

2.2. Food provisioning rate

We monitored food provisioning rates by placing an infrared-equipped camera inside the nestboxes for 1.5 h on day 9 post-hatching. Great tits usually resume normal feeding within less than 15 min after human disturbance [34]. The first 30 min after placing the camera was discarded and the subsequent 60 min used to assess male and female visits.

2.3. Field metabolic rate

Field metabolic rate (FMR) was assessed by using the doubly labelled water (DLW) technique [60]. When nestlings were 11 days old, adults were caught for the first time, weighed to the nearest 0.1 g, and injected intraperitoneally with 0.1 ml of a mixture containing 6.0003 g of 98.44% $H_2^{18}O$ and 3.0121 g of 99.9% D_2O . They were then kept in bags for around 30 min to allow isotopes to mix with the body water pool. Before release, birds were weighed and an initial blood sample was taken from the brachial vein. After on average 24 h (± 1.99 SD) later, they were recaptured, weighed and a second blood sample taken

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