

## Hormonal response of nestlings to predator calls

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### ABSTRACT

Chicks of altricial birds may perceive predation risk by acoustic cues produced by predators. This capacity involves changes to a less conspicuous behavior to avoid being detected and predated. However, little is known about the physiological mechanisms underlying this capacity. Potential mechanisms may involve corticosterone and testosterone, two hormones related to begging, an acoustic signal, which could be used by predators to locate and predate the nest. However, given the species-specificity of this relationship, it is difficult to make particular predictions. We manipulated perceived risk of nest predation in the common blackbird (*Turdus merula*) and analyzed nestlings' plasma levels of these hormones to look for nest predation risk effects. Our experimental manipulation showed hormonal changes in response to nest predation risk. Chicks under a high risk of nest predation reduced their corticosterone plasma levels but increased their testosterone levels in comparison with nestlings exposed to a low nest predation risk. We explain our results as mechanisms to reduce begging activity and discuss them within the framework of hormonal modifications in developing animals. These findings highlight the importance of studying nest predation from the unusually considered chick perspective and underlined the benefits from including physiological variables in the study of predator–prey interactions.

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### 1. Introduction

Nest predation is one of the main selective forces modulating avian life-histories [42]. Several studies have demonstrated that adult birds adaptively respond to the risk of nest predation by modifying their behavioral patterns (reviewed in [33,43]). For example, currently it is well established in birds that parents turn to a less conspicuous behavior (e.g. reducing their visits to the nest) in the presence of a potential nest predator [12,13,15,44,48]. Additionally, other papers highlight parental physiological changes like modifications in corticosterone (the main stress hormone in birds) levels to acute or chronic threats to the nests (e.g. [7,14,57,58,65] but also see [3]).

However, much less is known about the changes induced by predators in nestlings [53] despite the fact that nest predation has greater fitness consequences on chicks (being predated) than on parents (losing a single reproductive event). Recent studies showed that parents may modulate chick begging behavior in response to changes in nest predation risk, which can provoke their silence in the presence of a threat (a “switch off” strategy) or their begging calls under all-clear situations (a “switch on” strategy)

[8,38,39,49,50]. Even more, at least the chicks of one species, the white-browed scrubwren (*Sericornis frontalis*), seem to assess the risk of nest predation directly from its source and independently of their parents as nestlings of this species fell silent when they were exposed to the sound of a nest predator approaching [41]. This framework of behavioral changes in chicks in response to nest predation risk suggests that physiological alterations in offspring as well as in adults could exist. Indeed, Tilgar et al. [61] in one of the few studies exploring this possibility (the only using birds) showed indirect evidences of this effect of nest predation risk in the physiology of developing animals. They found increased corticosterone levels in nestlings of the pied flycatcher (*Ficedula hypoleuca*) following presentation of nestlings' distress calls repeatedly over several days. Nevertheless, despite evidences suggesting the benefits of including physiological variables in the study on predator–prey interactions [59], the studies exploring this topic are still very scarce.

Hormones are good candidates to study these physiological changes as they play an important role in the organization and activation of physiological and behavioral traits, and their levels are influenced by environmental factors [31,46]. Nestlings of many species modify their corticosterone (Cort) levels in response to stressful situations simulating a nest predation event (i.e. handling by researchers) [16,26,27,37,55]. This steroid hormone promotes survival via mobilization of endogenous energy and other

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physiological changes reviewed in [31,56]. Then, if chicks identify a potential nest predator as a threat to their survival, their cort levels should increase accordingly (prediction 1a). Alternatively, high levels of this hormone are also related to begging behavior [27,28,35] but also see [64]. Thus, considering that part of this behavior implies an acoustic signal used by predators to locate the nest [9,20,21,32,45], a reduction in nestlings' cort levels could be predicted too (prediction 1b). In addition, testosterone (T) is considered to control also part of the mechanism underlying begging activity, although the proposed relationship between T levels and begging is quite variable. Some studies detected a positive relationship showing that high levels of T increased begging [2,17,51] while others obtained the opposite pattern [18,19]. Then, we could expect an elevation (prediction 2a) as well as a reduction (prediction 2b) in T levels simultaneously to the changes in cort in order to reduce the acoustic cues given to predators through begging.

Most of the common blackbird (*Turdus merula*) populations suffer from a very high nest predation pressure [6,22,25,62], making this species an excellent model to study the effect of this selective force on chick's behavior and their associated physiological changes. To test the effect of nest predation risk on nestling's hormonal responses we simulated the presence of a magpie (*Pica pica*) in the vicinity of the nests using playbacks.

## 2. Material and methods

### 2.1. Study area and species

The common blackbird is a medium sized passerine widely spread throughout the Palearctic, which uses open nests to breed [5]. This study was conducted in the surroundings of Granada city (37° 10' N, 3° 36' W) in south of Spain, from early March to early July 2007. This is an area with many breeding blackbirds that suffer from a relatively high nest predation pressure reaching 80% of nest predated in some occasions [25]. We actively searched for nests in this area ( $n = 150$ ). Once a nest was located we visited it regularly (every 3 days) until fledge or predation to assess laying date, hatching date and number of fledging.

### 2.2. Manipulation of the nest predation risk and chicks sampling

When chicks were 8 days-old ( $\pm 1$  day) the perceived risk of nest predation was manipulated by simulating the presence of a magpie (*Pica pica*) in the surroundings of the nest. This corvid is a nest predator present in the area of study (pers. obs.). For this purpose, nests were exposed for 3 h to a playback (one 15 s magpie call per 3 min, TDK endless cassette, EC-6M) starting at daybreak. The recorder was moved every hour to simulate change in position by the predator. We used 7 different magpie call recordings to avoid blackbirds get used to them and the potential problem of pseudoreplication. The control treatment consisted in the same manipulation protocol as for the experimental treatment but playing no sound as we had previously tested that there are no significant differences for blackbird's reaction to woodpigeon (*Columba palumbus*) or no sound playbacks [24]. Nests were exposed to control or experimental treatments on consecutive days, with approximately half of the nests starting with the control ( $n = 20$ ) and the other half with the experimental treatment ( $n = 15$ ). Our experiment was made when chicks were 8 days-old, before they have the capacity to leave the nest. This allow us to be sure that our results reflect the normal behavior of nestlings. This is especially important given recent evidences suggesting important differences in antipredator behavior between nestlings and fledglings [40].

After the 3 h, half of the brood was sampled the day the nest was exposed to the control treatment and the other half the day

with the experimental treatment. Thus, all chicks were sampled at the same time of the day controlling for this potential confounding factor. Chicks sampled for each treatment were chosen randomly, usually sampling 1–2 chicks at a time depending on the brood size of a particular nest (mean brood size  $\pm$  SE =  $2.68 \pm 0.18$  chicks). Two blood samples (100–180  $\mu$ l each) were collected from the brachial vein using sterile needles and heparinized microcapillary tubes. The first sample was taken immediately after the end of the playback period, and the second after 30 min. We chose 30 min as the time for the second sample because previous studies on this species have shown that it is a good proxy for the maximum corticosterone levels [47]. Between sampling, chicks were kept unmolested in a cloth bag. All first blood samples were taken within 3 min following chicks' removal from the nest. Each nestling was weighted using an electronic balance ( $\pm 0.1$  g) after blood sampling for each treatment (day). Using this experimental procedure we managed to obtain blood samples from 90 chicks coming from 35 different blackbird nests.

Blood samples were kept in a portable fridge at 4 °C for up to 3 h. Then, blood samples were centrifuged at 13,000 rpm for 1 min. Plasma samples were stored at  $-40$  °C until radioimmunoassay analyses.

### 2.3. Hormone assays

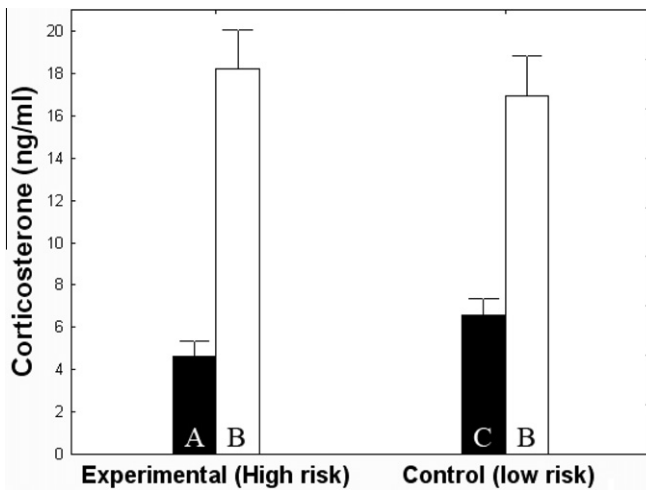
Cort and T levels in plasma were determined by radio immunoassay as detailed in Lormée et al. [36] and Chastel et al. [4] at the Centre d'Etudes Biologiques de Chizé (CEBC). Intra-assay coefficients of variation were 1.42% for cort and 3.08% for T ( $n = 3$  duplicates). The lowest concentration detectable was 195 and 68 pg  $\text{mL}^{-1}$  for cort and T, respectively.

### 2.4. Statistical analyses

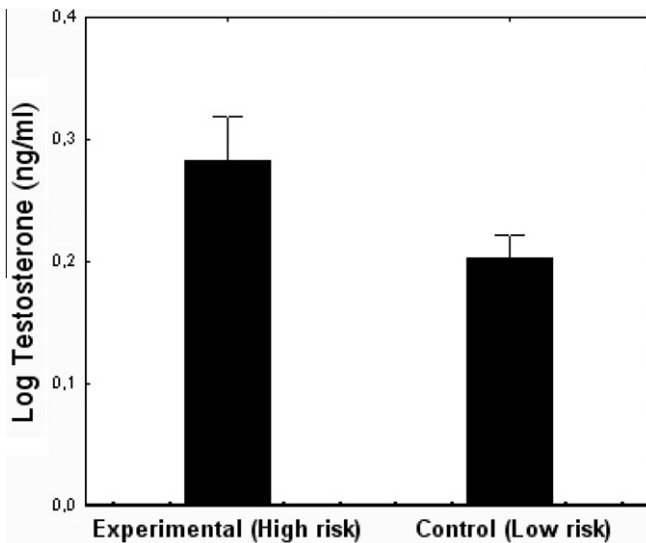
We used mixed linear models with fixed and random effects (Statistica 6.0). As nestlings share genes and the environment (the nest), the nest identity was always included in the models as a random factor. The predation risk treatment was included as a fixed factor and covariates (body mass, brood size and hatching date) were also added. Baseline cort level was also added as a covariate for the analysis of one variable (maximum cort level). The assumptions underlying the use of the linear model were systematically checked and the  $\log_{10}$ -transformation was applied when necessary.

## 3. Results

Baseline cort levels were significantly influenced by the treatment ( $F_{1, 29.5} = 4.64$ ,  $p = 0.04$ ) being lower in the experimental treatment (high risk situation) than in the control (low risk situation) fitting to prediction 1b (Fig. 1). In contrast, we observed no significant differences for the maximum cort levels ( $F_{1, 24.1} = 0.44$ ,  $p = 0.52$ ; Fig. 1), which on the contrary seemed to be positively explained by the baseline cort level ( $F_{1, 45.4} = 7.41$ ,  $p = 0.009$ ) and the nestling weight ( $F_{1, 31.2} = 5.14$ ,  $p = 0.03$ ). Brood size did not affect either baseline cort ( $F_{1, 28.5} = 0.72$ ,  $p = 0.41$ ) nor maximum cort ( $F_{1, 25.9} = 0.001$ ,  $p = 0.98$ ). With respect to the T levels, again we detected a significant effect of the treatment on plasma levels of this steroid ( $F_{1, 21.9} = 4.55$ ,  $p = 0.04$ ) showing the opposite pattern found for baseline cort levels: higher T levels in the experimental treatment (high risk situation) than in the control (low risk situation), thus, fitting to prediction 2a (Fig. 2). Additionally, we did not detect a significant brood size effect on T levels ( $F_{1, 20.8} = 0.02$ ,  $p = 0.88$ ).



**Fig. 1.** Nestling baseline (black columns) and maximum (open columns) corticosterone levels for each treatment. Bars associated to each column denote the corresponding standard error. Columns with different letters indicate significant differences at the  $p < 0.05$  level.



**Fig. 2.** Nestling testosterone levels for each treatment. Bars associated to each column denote the corresponding standard error.

#### 4. Discussion

The results of this study show that 8 days-old chicks modify their hormonal levels (cort and T) depending on the nest predation risk. This suggests that not only adults but also nestlings can adaptively alter their physiology in response to the threat of a potential predator.

Contrary to prediction 1a, the increased nest predation risk situation simulated with the magpie sounds induced a reduction in nestlings' baseline cort level and not a rise (Fig. 1). This is not surprising given the important costs in chicks' growth, immune response and cognition associated with the cort increase that would compromise future survival [28,29,30,55], specially if the frequency of the events that triggered this increase (i.e. listen to a potential predator) is high. Thus, it seems likely that chicks will rise their cort levels only in situations involving direct and imminent threats to their survival (i.e. a nest attack) when the benefits surpass the costs. This is supported by the nestlings' large increase

in cort in response to handling stress (Fig. 1), which would simulate a predation event.

In contrast, the reduction in baseline cort level under the high risk treatment matches perfectly with prediction 1b, that explained this modification to occur in order to silence the chicks. Begging is known to attract predators to the nests due to the acoustic cues given by nestlings when performing this behavior [9,20,21,32,45]. Moreover, high levels of cort have been related to increased begging [27,28,35] but also see [64]. Therefore, the down-regulation in cort levels associated with the presence of a potential predator (i.e. magpie) near the nest could reduce the number of acoustic cues produced, thus reducing nest conspicuousness and enhancing chicks' survival.

Our results seem to contrast markedly with those obtained by Tilgar et al. [61]. They found that pied flycatcher nestlings increased their cort levels when exposed to the sound of distress calls by other flycatcher chicks. But their manipulation reflects an imminent and direct threat to the nestlings, which would only hear such distress calls when their own nest has been located and it is being predated. Thus, similarly to adult birds they will benefit from an elevation of cort levels reviewed in [31,56] as expected by prediction 1a. Conversely, our experiment reflects a potential and indirect threat to nestlings (the predator is close to the nest but have not detected it already). Therefore, the reduction in cort levels not to reveal the nest location seems the best option for survival fitting prediction 1b. Furthermore, while Tilgar et al. [61] simulated a long term or chronic stress as they exposed flycatcher chicks to distress call 1 h over several days, our manipulation reflects more a situation of short-term or acute stress.

The observed increase in T levels for the experimental treatment fit to prediction 2a indicating that T modification could also be attributed in order to reduce begging activity (Fig. 2).

This is supported by the findings of some studies that showed a substantial decrease in begging due to experimental increases in T [18,19]. This is a likely possibility despite other papers have shown the opposite pattern: increased T levels increase begging intensity [17,51] because the action of T seems species-specific [16]. The rise in T levels could partially explain the reduction in cort levels observed in blackbird nestlings too, as both steroid hormones bind with the same binding globulin [10]. This indicates the possibility that the down-regulation observed in cort is a consequence of the increase in T rather than a response to the modification of nest predation risk itself. Indeed, no negative effects of T on growth or survival have been reported [1,23,54,60,63] and its effects on immunity are variable, with some studies reporting no effect while others finding some, and the possible influence of subtle effects [11,52]. This suggests that the costs for the same response would be much lower for the T than for the cort, considering the pleiotropic effects associated to the latter (see above). This cost perspective is especially important in developing organisms, like chicks, as even short-term changes in hormonal levels may alter the proper development and have important fitness consequences [34].

These hormonal responses apparently support previous findings that suggest the capability of nestlings to detect the presence of a nest predator and alter their behavior accordingly. Nevertheless, the modification of the nest predation risk also induces changes in parental behavior (i.e. giving alarm calls) to minimize the possibilities of nest detection by predators [8,38,39,49,50]. Because parents can also influence chicks' behavior in this way, it is difficult to discern whether nestlings respond directly to the predator presence or through mediation of their parents. Unfortunately we did not measure parental alarm calls to test this alternative hypothesis. However, independently of the acoustic signal used to trigger nestlings' responses, the relevant fact is that chicks adaptively modify their physiology in response to the current risk of nest predation.

To sum up, our results show that blackbird chicks adaptively adjust their hormonal patterns of cort and T depending on the nest predation risk, probably in order to reduce their begging activity and to avoid being detected by predators. However, it is not clear yet whether these hormonal changes are triggered directly by predators or their parents (i.e. giving alarm calls). These findings highlighted the importance of studying nest predation from the less studied chick point of view and underlined the benefits from including physiological variables in the study of predator–prey interactions.

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