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Animal behaviour

Plasticity of parental care under the risk of predation: how much should parents reduce care?

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Predation can be an important agent of natural selection shaping parental care behaviours, and can also favour behavioural plasticity. Parent birds often decrease the rate that they visit the nest to provision offspring when perceived risk is high. Yet, the plasticity of such responses may differ among species as a function of either their relative risk of predation, or the mean rate of provisioning. Here, we report parental provisioning responses to experimental increases in the perceived risk of predation. We tested responses of 10 species of bird in north temperate Arizona and subtropical Argentina that differed in their ambient risk of predation. All species decreased provisioning rates in response to the nest predator but not to a control. However, provisioning rates decreased more in species that had greater ambient risk of predation on natural nests. These results support theoretical predictions that the extent of plasticity of a trait that is sensitive to nest predation risk should vary among species in accordance with predation risk.

1. Introduction

Risk of predation on dependent offspring is often an important source of natural selection that shapes traits in both offspring and parent (reviewed in [1–3]). One trait that is thought to be sensitive to predation risk is the frequency with which parent birds visit the nest to provision offspring. Increased parental food delivery rates to offspring are a clear benefit that can influence offspring quality [4,5], but can incur costs by attracting predators and increasing the risk of offspring predation [6]. Temporal and spatial variation in predation risk should favour the evolution of behavioural plasticity, whereby parents reduce nestling provisioning rates when faced with an immediate increase in predation risk [7–11]. Yet, while such plasticity appears to be adaptive, withholding care also has costs, leading to the question of how much parents should reduce care when predators are present [1,12].

One possibility is that nestling provisioning rates should be reduced more in bird species at greater ambient risk of predation. The assumptions underlying this possibility are (i) the benefits of provisioning increase asymptotically, (ii) the risk of nest predation increases with increasing provisioning rates (*sensu* [6]) and (iii) the ambient cost function is steeper in species with more vulnerable nests (figure 1). Thus, when faced with an immediate risk, such as a predator in the vicinity of the nest, cost functions become steeper and favour a greater reduction in provisioning rates (figure 1). The magnitude of these reductions is predicted to be greater in species with higher ambient risk, because of their greater vulnerability to predators, relative to species with relatively safe nests (figure 1). While the true shape of these cost-benefit functions has not been described, comparing how species with different ambient risk respond to encounters with nest

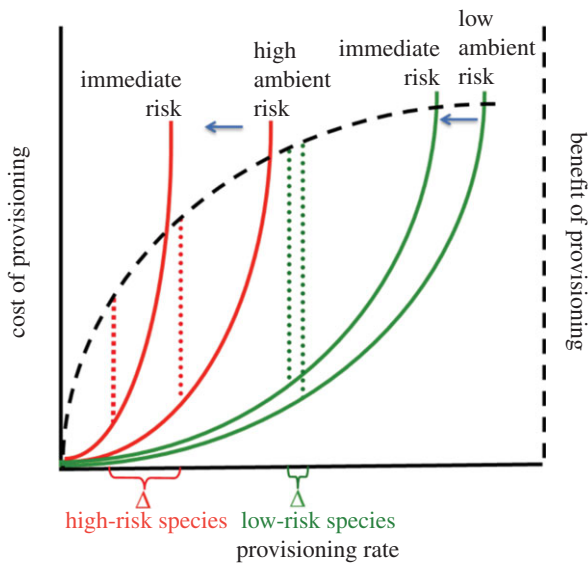


Figure 1. Conceptual depiction of possible optimum responses to an increase in the immediate risk of nest predation (i.e. predator near the nest) and the consequences for plasticity for two hypothetical species with differing levels of ambient risk. An optimal response is defined as one that maximizes the difference between benefit (dotted line) and cost (solid line). The cost represents the increase in predation risk with increasing provisioning rate. This cost is expected to increase more rapidly in species with higher ambient risk (e.g. exposed open-cup nests) than in species with lower ambient risk (e.g. cavity nests).

predators allows tests of these predictions and provides insight into the causes of behavioural plasticity (figure 1; [12]).

Alternatively, the degree of plasticity may be related to the mean trait value [13]. Because bird species at higher ambient risk of nest predation provision nestlings at reduced rates [8,14,15], they might be constrained in the amount of plasticity in provisioning rates; such parents are already feeding at low levels and any further decrease might cause serious food limitation to offspring [4,5] thereby constraining plasticity. Thus, these two alternatives yield opposite predictions for plasticity in parental care; species at greater risk of nest predation will exhibit larger reductions in provisioning (figure 1) versus smaller reductions because of low mean provisioning rates. Here, we test these two alternatives by examining how 10 bird species that vary along a continuum of ambient nest predation risk alter their provisioning rates in response to experimental nest predator presentations.

2. Material and methods

Study sites were high-elevation (2300 m elevation) mixed forest in Arizona (34° N, 111° W) and mixed subtropical forest in El Rey National Park, Salta Argentina (24° N, 60° W). We experimentally increased the risk of predation during the nestling period using vocalizations of a nest predator and followed the same protocol at both North American and South American study sites [16]. We used a double control method, where we had a temporal control (i.e. pre-stimulus observation period where parents provisioned without disturbance) followed by the presentation of either a control stimulus (i.e. non-threatening tanager) or a nest predator stimulus (i.e. jay). The experimental design consisted of a 90 min pre-stimulus control period followed by a 90 min presentation of either a nest predator (jay) or a non-threatening (tanager) control. Provisioning rates of parents were quantified from a blind approximately 15 m from

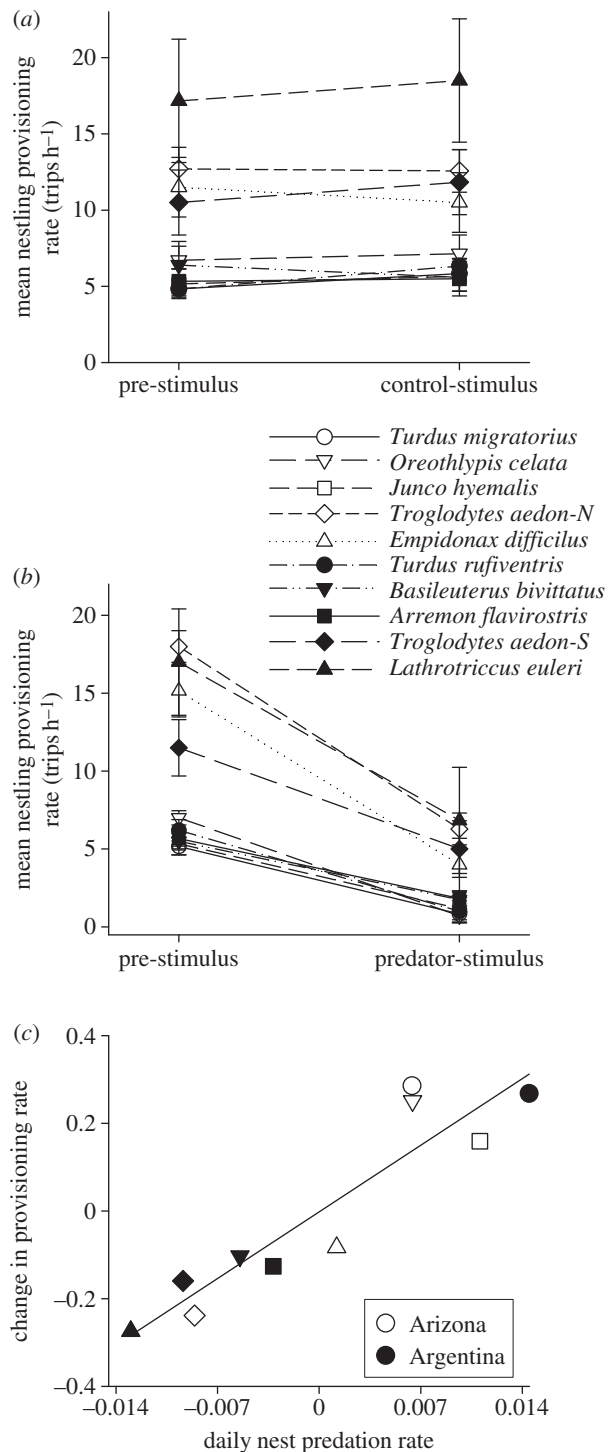


Figure 2. Parental provisioning responses to (a) control (tanager) versus (b) nest predator (jay) presentations. Shown are mean nestling provisioning rates (trips h^{-1}), for the pre-stimulus versus stimulus presentation periods. LSD *post hoc* tests revealed no difference in provisioning rates for the pre-stimulus tanager versus tanager stimulus ($p > 0.05$), and neither of these differed ($p > 0.05$) from the pre-stimulus predator (jay), but all three differed from the predator presentation ($p < 0.001$). (c) Partial regression plot (controlling for clutch sizes) between the per cent change in provisioning rates (degree of plasticity) in the face of an immediate threat and ambient risk measured by daily nest predation risk.

the nest. The perceived risk of nest predation was increased using taped vocalizations of phylogenetically related and common nest predators at both sites: Steller's jay (*Cyanocitta stelleri*) in Arizona, and plush-capped jay (*Cyanocorax chrysops*) in Argentina. Models (taxidermic mounts) and vocalizations were

used for the phylogenetically related western tanager (*Piranga ludoviciana*) in Arizona, and Sayaca tanager (*Thraupis sayaca*) in Argentina as controls, because they are common at each study site and represent no known risk to parents or young. Models of jays were not used because they caused extensive mobbing responses that obscured provisioning responses and so we restricted presentations to vocalizations. Models and speakers were placed approximately 8 m from the nest. To control for time of day and order of presentation effects, the tanager and jay presentations were made in a stratified random order. All presentations were made within 1 or 2 days of the nestling pin feathers breaking their sheaths to control for differences in developmental stage of young.

We focused on 10 species paired between Arizona and Argentina by phylogeny and ecology, listed as family (Arizona species, Argentina species): Tyrannidae (*Empidonax difficilis*, *Lathrotriccus euleri*); Turdidae (*Turdus migratorius*, *Turdus rufiventris*); Troglodytidae (*Troglodytes aedon aedon*, *Troglodytes aedon musculus*); Emberizidae (*Junco hyemalis*, *Arremon flavirostris*); Parulidae (*Oreothlypis celata*, *Basileuterus bivittatus*). The sample sizes of nests tested ranged from five to seven per species. These species were originally chosen to test parental responses to predation risk as a function of latitudinal differences in their clutch size [16]; however, these species also differ substantially in their ambient risk of nest predation and their mean provisioning rates [14]. The daily probability of nest predation was estimated from large samples of nests in Arizona and Argentina over multiple years to provide robust estimates of ambient risk [16,17].

We first tested whether parental responses differed between the two pre-stimulus control periods and the nest predator treatment (jay) and control (tanager) presentations. General linear models were used, with treatment (pre-stimulus tanager, tanager stimulus, pre-stimulus jay and jay stimulus; figure 2a) and species as fixed factors. Least significant difference (LSD) was used in *post hoc* tests of differences among the four treatment periods. We then calculated the relative change in provisioning rate as: (provisioning rate in the pre-stimulus control period – the provisioning rate in the jay presentation period)/(provisioning rate in the pre-stimulus control period). This percentage change in feeding rate was arcsine transformed prior to analysis. We tested the relationship between this relative change in provisioning rate and both ambient nest predation risk and mean provisioning rate using multiple regression; we included ambient nest predation risk, mean provisioning rate during the pre-stimulus control period and clutch size in the model and computed partial correlations. Mean clutch size of each species was included because temperate and subtropical relatives differ in clutch size, and these differences can influence provisioning responses of parents to predation risk [16]. Data deposited in the Dryad repository: doi:10.5061/dryad.0m480 [18].

3. Results

Parental provisioning rates differed among species and treatments (figure 2a,b), but the species by treatment interaction was not significant (*species*: $F_{9,200} = 23.6$, $p < 0.001$; *treatment period*: $F_{3,200} = 34.3$, $p < 0.001$; *species* \times *treatment*: $F_{27,200} =$

14.9, $p = 0.58$). The effect of treatment reflected significantly lower mean provisioning rates during the presentation of the jay stimulus than all three other periods (figure 2a,b); rates did not differ between any of the three control periods (i.e. pre-stimulus tanager, pre-stimulus jay or non-threatening tanager stimulus; figure 2a,b). Thus, temporal (pre-stimulus) and presentation (tanager) controls all were similar and verified that they acted as controls. By contrast, parental provisioning rates strongly decreased with the nest predator (jay) presentation (figure 2b).

The percentage change in provisioning rate between the pre-stimulus control period and the nest predator stimulus period was strongly correlated with the ambient risk of predation for these species, while controlling for clutch size (figure 2c; *nest predation*: $r_p = 0.92$, $p < 0.001$; *clutch size*: $r_p = 0.83$, $p = 0.006$). By contrast, the percentage change in provisioning rate was not related to the mean feeding rate of each species during the pre-stimulus period ($r_p = -0.44$, $p = 0.3$).

4. Discussion

The results clearly show that parents are sensitive to the risk of predation near the nest. Provisioning rates declined for all 10 bird species in two different geographical areas when vocalizations of a local nest predator were broadcast near the nest, compared with both temporal and model controls (figure 2a,b). This result alone is not surprising, as several studies have shown that parents reduce provisioning rates in the face of increased predation risk [7–11]. More importantly, our results show that the amount by which parents decreased provisioning (i.e. the degree of plasticity) was strongly related to the ambient risk of predation (figure 2c).

This increase in plasticity we observed with ambient risk of predation was opposite to expectations based on mean provisioning rates alone [13], given that provisioning rates varied inversely with predation risk ($r = -0.78$, $p = 0.008$; clutch size n.s.; also see [15]). Instead, we found support for the hypothesis that risk should change most for species with high ambient risk (figure 1), and these are the species that also have the lowest mean provisioning rates [15]. Consequently, parents of species with greater ambient predation risk appear more willing to incur short-term food costs to their young for the benefits of reducing predation risk. Thus, the question of how much parents should reduce care in the face of immediate predation risk is answered in part by the ambient risk experienced by a species.

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