Temporal trade-offs between nestling provisioning and defence against nest predators in blue tits

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Offspring provisioning and nest defence are important forms of parental care. In birds, parents that engage in nest defence behaviour have to interrupt nestling provisioning with potentially harmful consequences for offspring growth and condition. To maximize fitness, parents should trade off optimal levels of offspring provisioning versus nest defence, but relatively little is known about how parents allocate their time between these two activities and how parental decisions to postpone provisioning vary as a function of the intensity of nest predation risk. We found that pairs of blue tits, Cyanistes caeruleus, adjusted parental care behaviours according to perceived immediate risk levels by switching from offspring provisioning to nest defence. In the presence of a direct nest predation threat, parents interrupted offspring provisioning for longer than in response to a novel object close to the nest, but still gradually resumed provisioning activity, probably because of a decrease in perceived predation risk over time. By increasing their provisioning effort once the immediate threat had diminished, parents compensated at least partly for the lost provisioning opportunities during high-risk situations. Hence, by adaptively adjusting the temporal trade-off between different parental care behaviours according to the perceived risk, blue tits are presumably able to mitigate potential negative long-term consequences of interruptions in provisioning during high-risk situations for offspring growth and condition.

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Offspring provisioning systems have become a model for the behavioural study of adaptive parental investment (Clutton-Brock 1991; Royle et al. 2012), biparental cooperation (Houston et al. 2005; Harrison et al. 2009), and parent–offspring conflict and the evolution of begging signals (Wright & Leonard 2002; Hinde & Kilner 2007; Smiseth et al. 2008). However, other important aspects of parental care, such as antipredator defence of offspring, are rarely studied alongside offspring provisioning. This is surprising, because these activities should trade off with, or interrupt, provisioning because of limitations in time and energy. Such trade-offs

could be critical for adaptive levels of provisioning effort and optimal behavioural responses to changes in conditions (Markman et al. 1995, 1996; Rauter & Moore 2004).

In birds, predation is an important cause of nest failure (Ricklefs 1969), and birds are able to minimize nest predation risk through plastic behavioural responses towards the actual threat level (Lima 2009; Martin & Briskie 2009). Besides nestling provisioning, nest defence is an important form of avian parental care (Shields 1984), which can range from vocal mobbing from a safe distance to physically attacking the predator, and is assumed to have evolved to reduce losses of nestlings to nest predators (Montgomerie & Weatherhead 1988). This assumption is confirmed by numerous studies, showing a positive relationship between nest defence behaviour and nest success (e.g. Greig-Smith 1980; Blancher & Robertson 1982; Markman et al. 1996).

Even though antipredator behaviour might be beneficial in terms of immediate nestling survival, it also incurs costs for parents and offspring that might depend upon the type of nest predator (Lima 2009). For example, nest defence against predators that also

prey upon adult birds would represent a relatively high potential fitness cost, because of the additional risk of adult predation. In contrast, the presence of a nest predator that only consumes nestlings represents little direct risk to the parents, but defence might be costly in terms of offspring production because of harmful interruptions to nestling provisioning. Parents therefore face the dilemma of trading off the two mutually exclusive behaviours of offspring provisioning and nest defence. Doing so allows them to maximize the productivity of the current nesting attempt while taking into account effects on their future reproductive output (i.e. the parent's ability to invest in future broods: Trivers 1972). One way that parents could do this is to adjust provisioning activity over time according to the variation in nest predation risk.

Despite the large number of studies on immediate antipredator nest defence or mobbing, relatively little is known about the temporal patterns of alternative parental care behaviours in different risk situations. For instance, perceived predation risk is expected to differ before, during and after the encounter with a nest predator (Tilgar et al. 2011). Even during the presence of a predator, the response of the parents should diminish over time owing to adaptive habituation (Rankin et al. 2009). Hence, to minimize both the costs of potential nest predation and nestling starvation, parents should allocate different amounts of time to provisioning and nest defence according to the risks involved (Lima 2009). During high predation risk situations, parents should reduce nest visit rates and/or engage in vigorous nest defence behaviour, whereas parents should maintain nestling provisioning at a rate closer to normal levels when nest predation risk is relatively low (Martin & Briskie 2009). This expectation is confirmed by a number of empirical studies showing that increased risk of predation on dependent offspring can cause parents to reduce their provisioning rate temporarily, if only to reduce the chances of nest detection by the predator (e.g. Ghalambor & Martin 2000, 2001; Eggers et al. 2005; Fontaine & Martin 2006; Peluc et al. 2008). However, to understand the temporal trade-off between provisioning and nest defence, we also need to know how the perceived predation threat changes over time, that is, how quickly parents habituate to the threat and resume provisioning the young in the nest.

The temporal trade-off between nest defence and offspring provisioning will also depend upon the underlying mechanisms of predator recognition and the individual discrimination abilities needed to produce adaptive differences in parental responses to different types of predation threat. Predator models have been shown to elicit antipredator responses similar to those of live predators (Curio 1975), and there has been a long history of investigating (functional) differences in parental responses to different types of model predators (Lima 2009; Martin & Briskie 2009). In contrast, engaging in extended nest defence behaviour against a harmless (novel) object is expected to be nonadaptive as it does not increase nest survival, but nevertheless incurs costs in terms of lost provisioning opportunities. To be able to show adaptive behavioural responses to nest predation threats, parents need to differentiate correctly between different levels of threat represented by known nest predation threats versus novel but harmless situations, and to adjust the scale of their response and its decline over time if the situation persists. In this study, we aimed to investigate whether actual predator recognition is involved in driving such parental responses, that is, whether parents behave differently towards a taxidermic model of a real nest predator or whether they merely respond to new objects around the nest (Curio 1975).

We investigated the responses of provisioning pairs of blue tits, *Cyanistes caeruleus*, towards a taxidermic model of a great spotted woodpecker, *Dendrocopos major*. This species is a typical nest predator of Eurasian cavity-nesting birds (Löhrl 1972) and can inflict heavy losses on nests (Curio & Onnebrink 1995). In contrast, it represents little mortality risk to adult birds (Curio 1975). The typical nest defence behaviour of great tits, *Parus major*, and blue tits towards the presence of a woodpecker close to their nest consists of extended vocal mobbing (largely 'churr' calls) combined with frequent movements between perches, thereby rarely approaching the predator closely (Onnebrink & Curio 1991). Parental alarm calls might distract predators away from the vulnerable offspring and/or might warn nestlings about the predation risk (Harvey & Greenwood 1978; Greig-Smith 1980). We investigated in detail the temporal trade-off between nest defence and provisioning behaviour in blue tit pairs before, during and after an encounter with a model of this potential nest predator. We also explored whether blue tits are able to recognize a potential nest predator by comparing parental responses to a model predator and to a novel but nonthreatening object (a red rubber ball).

METHODS

Study Site and General Field Procedures

The study was carried out during the breeding season of 2011 on a nestbox population of blue tits in southern Germany (Westerholz, 48°08′N, 10°53′E). The Westerholz forest mainly consists of mature oak trees, *Quercus* sp. (for more details see Schlicht et al. 2012), the preferred habitat of blue tits (Gibb 1954). Adults were caught inside the nestbox during nestling provisioning when nestlings were 9 or 10 days old. Unbanded birds were fitted with a numbered metal band and a unique combination of three colour bands and equipped with a uniquely coded passive integrated transponder (PIT) tag (EM4102 ISO animal tag 134.2 kHz ISO, 8.5 mm × 2.12 mm, 0.067 g) following procedures detailed by Nicolaus et al. (2008). All nestlings were banded and measured when they were 14 days old.

Automated Recording of Provisioning Behaviour

Provisioning behaviour of the parents was recorded on 4 consecutive days at 48 nestboxes with automatic nestbox recording devices when nestlings were between 11 and 14 days old. For nestboxes where nestlings were processed less than 2 h before the planned data recording, we collected data on day 15 instead ($N = 14$ nestboxes), to ensure that nestling processing at day 14 did not affect our measures of control feeding rate. The recording device consisted of an antenna around the entrance hole (PIT tag reader), one light barrier inside and one outside next to the nestbox hole, a power supply and a data logger placed on the ground underneath the nestbox (for technical details see Schlicht et al. 2012). The sequence of activation of the two light barriers indicated the direction of the movement of a bird, allowing differentiation of entries and exits. Every time the bird passed through the nestbox hole the PIT tag was read, thus determining the identity of the bird entering or leaving the nestbox. However, owing to variation in sunlight reflection, light barriers sometimes did not work properly. Consequently, we checked all recorded data files to determine entry and exit times of PIT-tagged birds. We excluded trials (for a definition of trial see below) with unreliable data (i.e. with more than one nonassigned visit) from the final data set. In total, 33 of 288 control trials, 13 of 144 red ball trials and eight of 147 woodpecker trials were excluded from the analysis, resulting in a total sample size of 2596 visits for control day 1, 2826 for the red ball treatment day, 2394 for the woodpecker treatment day and 2609 for control day 2. We used nest visit rate as a proxy for feeding rate, as there is little variation in prey sizes and nonfeeding visits are rare at this stage in the nestling period (Kluijver 1950; Eguchi 1980; Nur 1984). Video recordings from 52 nests further showed prey delivery