



Nestling use of alternative acoustic antipredator responses is related to immune condition and social context



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Birds present a variety of antipredator responses, including the use of acoustic signals that may be directed to other individuals or to the predator. We tested competing hypotheses regarding antipredator responses by analysing patterns of variation in the use of distress calls in campo flicker, *Colaptes campestris campestris*, nestlings. More specifically, we tested whether immune response and social context (presence or absence of other individuals of the social group) were associated with variation in use of acoustic signals in response to human handling. Individuals with higher immunocompetence used proportionally more harsh, low-pitched calls ('scream' notes) than individuals with lower immunocompetence, while the latter used mostly tonal, high-pitched calls ('week' notes); in both cases there was no influence of the social context on call type. Individuals responded to the social context by giving fewer scream notes and week notes in the presence of adults of the social group than when the adults were absent. Although playbacks are necessary to determine the function of the calls, our results indicate that campo flicker nestling antipredator calls could be used to attract other individuals of the group to help defend the nestling. Also, the use of proportionally more scream notes by healthier individuals suggests that these notes could act as an honest signal of the nestlings' physiological condition.

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The use of acoustic signals is a versatile form of communication, with some species of birds having a diverse range of calls in their repertoire (reviewed in Marler, 2004). This diversity in call types is thought to be shaped by selective pressures acting upon both signallers and receivers, as both parties may benefit from the information exchange when there is consistency between the signal and the context in which it is presented (Bradbury & Vehrencamp, 2011; Font & Carazo, 2010; Maynard Smith & Harper, 1995, 2003). Information encoded in signals may be related to the environmental or social context perceived by an individual, its physiological condition or motivation, or a combination of these (Bradbury & Vehrencamp, 2011; Carazo & Font, 2010; Font & Carazo, 2010; Marler, 2004).

One of the contexts wherein signal emission is commonly observed is in the presence of predators. In birds, acoustic antipredator responses are mainly characterized by alarm and distress calls (or fear screams). Alarm calls are vocalizations given in a

context of danger, such as in the presence of a predator (Brémond & Aubin, 1990; Marler, 2004). Although distress calls can be considered a type of alarm call, they present certain distinctions such as being given when the signaller and the predator are in close proximity, including when the signaller has been captured (Hogstedt, 1983; Inglis, Fletcher, Feare, Greig-Smith, & Land, 1982). Distress calls are also extremely loud and harsh, usually with long and broadband notes, while other alarm calls usually have narrower frequency bands and a higher pitch (Hogstedt, 1983; Inglis et al., 1982; reviewed in Marler, 2004). These characteristics provide obvious means to identify these calls for most species. The information contained in these signals and the selective pressures involved in their evolution, however, are unclear.

One of the many possible functions of antipredator calls is to warn the predator that it has been detected, discouraging it from pursuing the prey (Bergstrom & Lachmann, 2001). Another suggested role is to warn kin of the presence of a predator, so they can seek cover (Sherman, 1977). These calls may function to attract other individuals to the site, including the parents of juveniles (Perrone, 1980), predators other than the one causing distress (Hogstedt, 1983; Koenig, Stanback, Hooge, & Mumme, 1991; Perrone, 1980), and heterospecifics (Aubin, 1991; Chu, 2001; Greig-Smith, 1984), thus generating confusion or distraction and

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allowing the prey to escape its predator. Furthermore, distress calls could function as an honest signal of quality of the potential prey, indicating to the predator its condition and ability to flee (Laiolo, Tella, Carrete, Serrano, & Lopez, 2004; Laiolo et al., 2007). Finally, distress calls could startle the predator, causing it to release the prey (Conover, 1994).

The use of alarm and distress calls is widespread among birds (Hogstedt, 1983; Marler, 2004), although there is considerable variation in the use and acoustic structure of the calls. In some species, alarm and distress calls vary in note composition, pitch or rate of production according to the type or distance of a predator (e.g. Branch & Freeberg, 2012; Ficken, 1990; Leavesley & Magrath, 2005; Stone & Trost, 1991; Suzuki, 2012; Zachau & Freeberg, 2012), consequently carrying additional information to conspecifics about the degree of risk (Ficken, 1990). This flexibility in fine-tuning signals has great potential for adaptive evolution, since inappropriate signalling in this context can be extremely costly for an individual's fitness (Caro, 1995).

Nestlings of many bird species utter distress calls when handled by humans (e.g. Perrone, 1980). In our study species, the campo flicker, *Colaptes campestris campestris*, nestlings being handled by humans use antipredator calls that present notes that typically characterize distress calls (loud and harsh 'screams') and notes that sound very similar to a 'week' call (tonal, harmonically structured, and with slightly modulated fundamental frequency) presented by adults of the species (Goedert 2010) and by other congeneric species (Short, 1972). Such flexibility provides an ideal opportunity to test the adaptive significance of these calls, as the study of plasticity in behaviours is important to understand and predict their evolution (Mazer & Damuth, 2001). Although most of the studies on antipredator strategies are focused on adults, nestlings are particularly vulnerable to predators. In tropical areas, nest predation is the overall main cause of nest failure, whereas adults have high survival rates (reviewed in Stutchbury & Morton, 2001).

In this study, we investigated how acoustic signals are used as antipredator responses by campo flicker nestlings. We focused on two questions. First, is the use of differently structured calls a condition-dependent response? Previous studies have suggested that the harshness of distress calls can be an honest signal of the signaller's condition (e.g. Laiolo et al., 2004; Laiolo et al., 2007). If this is the case for campo flicker nestlings, we expected individuals in better condition to use more scream notes (harsh, broadband notes) relative to week notes (tonal notes) in their calls.

Second, is calling rate dependent on the social context? If calls are directed to conspecifics, we would expect nestlings to adjust the rate of calling in relation to the presence of adults from their social group. If calls are directed to other receivers, possibly the predator or other predators in the vicinity, then we would not expect a difference in calling rates when adults from the social group were nearby and when they were not.

Considering the high degree of sociality of campo flickers (Dias, Webster, Goedert, & Macedo, 2013) and the high degree of relatedness among individuals of a social group (Dias, Macedo, Goedert, & Webster, 2013), there are at least two possible interpretations for the function of the calls if these are directed to other individuals of the social group: (1) to signal the presence of predators so that the genetically related individuals can seek cover (warn kin hypothesis; Inglis et al., 1982; Sherman, 1977); and (2) to attract other individuals that could mob the predator (cry for help hypothesis; Hogstedt, 1983; Perrone, 1980; Rohwer, Fretwell, & Tuckfield, 1976). As these two possible interpretations generate competing predictions for calling rates depending on the presence of conspecifics (as proposed by Branch & Freeberg, 2012), the suggested functions can be tested: if calls function to warn kin of the presence of predators, nestlings should show higher calling rates when adults

Table 1

Characterization of campo flickers in this study, indicating number and sex of nestlings per social group, number of adults in the social groups and the age at which nestlings were recorded

Social group	Number of adults	Number of offspring			Age (days) of nestlings when recorded
		Males	Females	Total	
1	3	2	3	5 ^{*,†}	23
2	2	1	1	2 [*]	23
3	3	1	1	2	24
4	2	1	2	3 [‡]	24
5	2	1	0	1	24
6	2	3	1	4 [‡]	25
7	2–3	1	3	4	24
8	2	1	2	3	24
9	3	0	1	1	24
10	4	1	1	2	24
11	2	1	2	3	24
	Total	13	17	30	

* Audio recording was missing for one offspring in the group and the individual was excluded from the analyses.

† Phytohaemagglutinin (PHA) data were missing for two offspring and both individuals were excluded from the first analysis.

‡ PHA data were missing for one offspring and the individual was excluded from the first analysis.

of the social group are nearby; however, if calls function to attract other individuals to the nest, we would expect nestlings to present lower calling rates when adults of the social group are nearby.

METHODS

Study Species and Field Site

The campo flicker is a terrestrial Neotropical woodpecker endemic to South America (Short, 1975, 1982; Sick, 1997), recognized as the subspecies *campestris* at the northeastern portion of its distribution (northeast Brazil to central Paraguay; Short, 1972). The campo flicker is a facultative cooperative breeder, with a highly complex social structure (Dias, Macedo, et al., 2013). Social groups range from two to five individuals during the breeding season, with all individuals engaging in reproductive activities and defence of group territories, which range in size from approximately 20 to 80 ha (Dias, Webster, et al., 2013).

We conducted this study during the breeding season (June to December) of 2009 at Fazenda Água Limpa (15°57'S, 47°56'W) in central Brazil, a site composed of a variety of typical cerrado (Brazilian savannah) vegetation types. The study population had been monitored for 2 years prior to this study, during which time we mist-netted and marked individuals with unique combinations of colour bands and identified social groups and territories (see Dias, Webster, et al., 2013 for details). A social group was considered as two or more individuals inhabiting a territory and showing territorial defence behaviours such as group displays.

Fieldwork

During the breeding season, we searched territories for active nests. Campo flickers are cavity nesters, nesting preferentially in termite mounds, but using tree cavities in territories lacking these structures (Dias, Webster, et al., 2013). We monitored nests every 2–3 days to check for the presence of eggs, and daily when eggs were close to hatching. Nestlings were captured and handled 23–25 days after the first chick hatched (nestling period lasts 29 days on average; Dias, Webster, et al., 2013). We measured the cell-mediated immunocompetence response of each nestling as an estimate of individual condition, evaluated based on skin swelling in

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