



Non-vocal communication as an anti-predator strategy in scaled doves (*Columbina squammata*)

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Abstract

Different strategies have evolved in response to predation pressure. Many species use acoustic signals to communicate about the presence of predators, and some of them use non-vocal sounds. Here, we evaluated the role of the non-vocal sound produced by scaled doves (*Columbina squammata*) during escape takeoffs. Initially, we investigated the context of the non-vocal sound production to assess the effects of natural threats on individuals' escape response. Then, we used simulated attacks (a direct running movement toward the focal individuals) to confirm the preliminary observations and to evaluate how position in the group affects escape response and vigilance. For both the observational and experimental parts, we registered, among other variables, the occurrence of takeoff flight, if it was followed by a production of non-vocal sound, the position of the individuals within the flock and their response (e.g., stay, flew, vigilance). We observed that both solitary and flocked individuals produce non-vocal sounds during takeoff flights, although it was more commonly registered for flocks. The production of the non-vocal sound elicited a faster escape response on flock members, and individuals at the center of the flock showed a higher probability to takeoff. The results suggest that the non-vocal sound may signal information about predation risk and that it may be directed both to conspecifics and to the predator itself. Our results therefore contribute to the understanding of the evolution of mechanical sound production in birds and shed some light on its function as a communication signal, especially under a predation context.

Keywords Acoustic communication · Alarm signal · Mechanical sound · Non-vocal sound · Predator–prey communication · Trill

Introduction

Predation has been considered one of the main factors shaping the evolution of social behavior (Alexander 1974; Rubenstein 1978; Spieler 2003; Dittmann and Schausberger 2017). Despite other associated costs, sociality has been demonstrated to increase the chance of survival among different taxonomic groups, especially under higher risk of predation (Hill and Lee 1998; Sorato et al. 2012; Schmitt et al. 2014; Gardner et al. 2016).

The speed at which information about predation risk is exchanged in social groups depends on several factors, such as group structure, perceived predation risk, average distance between individuals, environment condition, etc.

However, information exchange is expected to be more rapid in smaller groups, promoting a shorter reaction time (Lima 1994; Quinn and Cresswell 2005; but see Martín et al. 2006; Fernández-Juricic et al. 2009; Beauchamp 2012). A study conducted with flocks of common redshanks (*Tringa totanus*) demonstrated that birds in smaller flocks, closest to the potential predator and which were close to other group members initiate the flight earliest within a flock (Hilton et al. 1999).

Despite the vast knowledge about the advantages of social living, there is much to know about the real roles and benefits of signal production within groups, especially under predation risk. This is mainly because of the costs of this behavior to the producer (e.g., may work as a cue for predators about its location; Wheeler 2008; Putman and Clark 2015). Signals may have evolved to dissuade the predator from attacking after detecting the signaler (Hasson 1991; Clark 2005; Alvarez et al. 2006), or may be directed to conspecifics to warn about potential predators (Seyfarth et al.

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1980; Fichtel and Kappeler 2002), or both. Signals produced by the bonaire whiptail lizard (*Cnemidophorus murinus*), for example, are interpreted as an attempt to inform the predator that it was spotted (Cooper et al. 2004). On the other hand, signals produced by Columbian ground squirrels (*Spermophilus columbianus*) significantly increased the vigilance of conspecifics in the presence of a potential predator, suggesting that the signal was directed to other group members (Fairbanks and Dobson 2007).

Among birds, communication signals are commonly produced by displaying parts of the body (visual stimulus), as observed in turquoise-browed motmots (*Eumomota superciliosa*), in elegant trogons (*Trogon elegans*) and in hoopoes (*Upupa epops*) (Murphy 2006; Bitton and Doucet 2014; Ruiz-Rodríguez et al. 2017) or through vocal structures, as observed in many species such as in red jungle fowls (*Gallus gallus*) (Collias 1987), in Carolina chickadees (*Poecile carolinensis*) (Soard and Ritchison 2009) and in tufted titmice (*Baeolophus bicolor*) (Courter and Ritchison 2010). In addition, some animals may use parts of their bodies to produce mechanical sounds (non-vocal sounds, e.g., whistles, trills), as observed in the club-winged manakin (*Machaeropterus deliciosus*) (Bostwick et al. 2010), broadbills (*Smithornis rufolateralis* and *S. capensis*) (Clark et al. 2016) and the red-billed streamertail hummingbird (*Trochilus polytmus*) (Clark 2008). Non-vocal sounds, considered to have a warning role during escaping behavior, have also been identified in several columbids, such as the inca dove (*Columbina inca*; Johnston 1960), mourning dove (*Zenaida macroura*; Coleman 2008), rock pigeon (*Columba livia*; Niese and Tobalske 2016), and crested pigeon (*Ochyphaps lophotes*; Murray et al. 2017).

Acoustic signals are considered as one of the main mechanisms of communication, especially for their range potential (Smith and Harper 2003). In particular, the role of non-vocal sounds seems to be dependent on adaptive selections (Prum 1998; Clark and Prum 2015), but so far this communication channel is poorly known. Recently, Murray et al. (2017) have demonstrated using playbacks and feather removal experiments that modified feathers of the crested pigeon are used as a reliable non-vocal alarm signal after a potential threat. This reinforces the need to comprehend the evolution of this type of communication among species, especially in situations of high predation risk, evaluating its effects on group coordination (Niese and Tobalske 2016).

Recognizing if a species has the ability to intentionally modulate a non-vocal sound which has evolved for a communication function (i.e., voluntariness) is obviously not an easy task (Bostwick and Prum 2003; Clark 2016). The identification of specialized morphology and behavior or the use of appropriate experiments may help to produce unequivocal evidence for voluntariness. Despite that, basic information about the context of non-vocal sound production

and the response of conspecifics is unknown for most species. In pigeons, the ability to produce subtle modifications of wing kinematics during the wing trill emission suggests that the production of the non-vocal sound may be voluntary (Clark 2016). The scaled dove (*Columbina squammata*) is a small columbid widely distributed in the Neotropical region. Among its main characteristics, its sociality stands out, together with the cryptic coloration and the production of a loud mechanical wing trill during takeoff flight, which may not be emitted under certain circumstances (Sick 1997; Dias 2006). Here, we evaluated the role of the trill produced by the scaled dove through observational recording and manipulation procedures. For this purpose, we tested the following hypotheses: (1) the non-vocal sound is used to communicate about situations of potential danger; thus, it is expected to be more frequently produced during escape takeoffs; (2) the non-vocal sound is directed to conspecifics, so it is expected to be produced in flocks but not in solitary conditions; (3) the non-vocal sound is interpreted as an alarm information by other flock members, and consequently it should promote escape responses on conspecifics; and (4), in flocks, individuals closer to the non-vocal sound producer should present faster escape responses in comparison to further ones.

Materials and methods

Study area

The study was conducted on the campus of the University of Brasilia, located in the central region of Brazil. The vegetation of the area is highly modified, composed of small grasses and scattered trees, surrounded by buildings of the institution. The presence of domestic animals (e.g., dogs and cats), car traffic and other natural predators (e.g., *Elanus leucurus*, *Falco femoralis*, *Gampsonyx swainsonii*) are the main threats faced by the birds in the area. The observations and recordings were conducted during the years of 2015 and 2016 between 0730 and 1100 hours, Brasilia time.

General procedures

Active searches were conducted to locate scaled dove individuals, both in flocks and solitary. After locating the individuals, we approached smoothly (trying not to disturb the natural behavior) staying around 15 m away to conduct the observations. The focal sampling initiated when the individuals were seen foraging, drinking water or resting on the ground. The data were registered both from personal observation and through video recordings. The video recordings were made with a 5-megapixel digital camera (Bright 0372 HD) supported by a tripod.

After the field procedures, all the video recordings were analyzed to assure the behavior of all flock members were individually considered. The study area has a large population of the scaled dove, and this may have helped to avoid pseudoreplication, since the birds were not individually marked. We measured to the nearest millimeter the width of the six outer primaries of two individuals to investigate the presence of any morphological adaptation for sound production. The width was measured at 2.5 cm from each feather tip.

Recording and sound analysis

We conducted audio recordings of individuals' non-vocal sounds using a digital Marantz PMD 660 recorder (16-bit precision and 44.1 Hz sampling rate), coupled to a Sennheiser K6/ME66 unidirectional microphone. Recordings were made between 0700 and 1100 hours. We analyzed the non-vocal sounds using the Raven Pro 1.5 (Bioacoustics Research Program 2014). We selected recordings of five different individuals with low background noise for the analysis, but also filtered out background sound below 400 Hz. We measured (1) the pulse period (time between the beginning of two successive pulses), (2) the pulse rate (Hz) and (3) the peak frequency (the frequency with the highest energy). Measurements were made on spectrograms with a Hann window of 512 samples, a hop size of 2.13 ms and with an 80.1% overlap.

Part 1: Context of non-vocal sound production

To understand the natural context of the non-vocal sound production, we conducted animal and group focal observations for 30 min or until one of the individuals initiated a takeoff flight. For each focal unit, we recorded the flock size at the beginning of the observation, the presence of a potential threat (yes or no) and the occurrence of takeoff flight (yes or no). If any individual fled during the observation period, we registered whether or not it was followed by the production of a non-vocal sound (which is loud and can be heard several meters away), and if it stimulated an escape response and vigilance behavior of other group members (yes or no). Vigilance behavior was defined as any moment that the individuals lifted their head upward while looking around. Additionally, for flocks, we registered the position of the individuals within the flock to investigate the role of spatial position (central or periphery) and also the response time of each flock member to the takeoff flight. We considered response time as the interval between the takeoff of a flock member and the response of each of the other members.

Part 2: Simulation of predation risk

After concluding the first part of the study, we began to evaluate the effects of simulated attacks on dove behavior. After locating the individuals, we registered the flock size and approached them, staying at around 15 m distance. After waiting 15 s, the simulated predation attack was performed. The simulations were conducted through a direct and steady running movement toward the center of the evaluated unit (flock or solitary individual) by one of the researchers (P.P.A.). After the simulation, the same variables previously described in Part 1 were registered (the occurrence of takeoff flight, production of non-vocal sound, the position of the individuals within the flock, the response time of each flock member to the takeoff flight and whether or not it stimulated vigilance behavior in other group members). Again, for flocks, the video recordings were used to quantify the response time (s) for each flock member after the takeoff flight and were also used to record the spatial position of flock members during that moment.

Statistical analyses

To test our hypothesis, the non-vocal sound production (yes or no) was fitted as a response term in a generalized linear model (GLM) with binomial family where the occurrence of a potential threat (yes or no) and the social organization (flocks or solitary individuals) were fitted as explanatory variables. Similarly, the vigilance (yes or no) and flight response (yes or no) of the focal birds, after the takeoff of any flock member, were fitted as a response term and the production of non-vocal sound (yes or no) was fitted as an explanatory variable. The effect of the non-vocal sound production in flock response time (s) was evaluated fitting a GLM with a Poisson family. To determine whether flock position influenced the vigilance response (yes or no), flight response (yes or no) and response time (s), we fitted a generalized linear mixed-effects models (GLMMs) with flock ID included as a random effect. For this analysis, we used the lme4 package (Bates et al. 2015). We used likelihood ratio tests to compare nested models of increasing simplicity. All statistical analyses were carried out in R v.3.4.1 (R Core Team 2017).

Results

Morphology of primary feathers and wing trill structure

It was not possible to visually identify a clear modification on the six outermost primary feathers (P10–P5; Fig. 1a, b). Despite that, the three outermost feathers (P10–P8) are

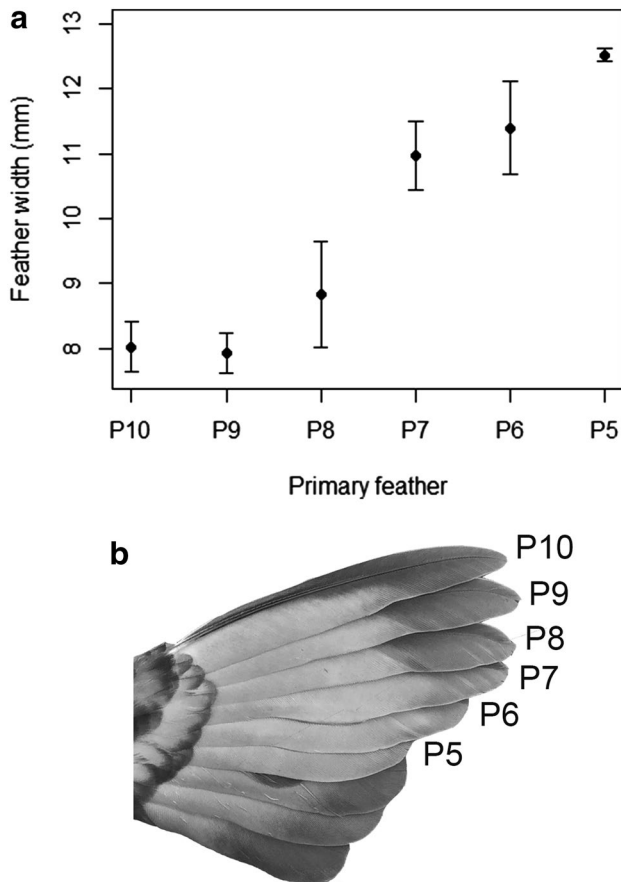


Fig. 1 **a** Feather average width of the six outermost primaries (P10–P5) of the scaled dove (*Columbina squammata*) and **b** a scaled dove (*Columbina squammata*) spread wing with the six outermost primaries labeled

narrower than the adjacent ones and it possible to see a round shape on the central portion of the P7–P5 feathers. The wing trill produced by the scaled dove was composed of a sequence of repeated notes with an average pulse period of 0.058 ± 0.004 s (mean \pm SD) and a pulse rate of 17.24 ± 1.10 (mean \pm SD). The average observed peak frequency was 5205.20 ± 532.74 kHz (mean \pm SD, Fig. 2).

Part 1: Context of non-vocal sound production

During this observational section, we evaluated 101 solitary individuals and 44 flocks (range 2–3). The average observation time (s) was 260.99 ± 356.15 (mean \pm SD). In most cases ($n=141$), the solitary individuals and flocks fled within the observation time. For those individuals and flocks, 57% ($n=80$) voluntarily left the area without being disturbed. All individuals and flocks exposed to a potential threat (e.g., approaching predator) immediately left the area. The production of the non-vocal sound was influenced by whether or not the individuals were gathered in flocks

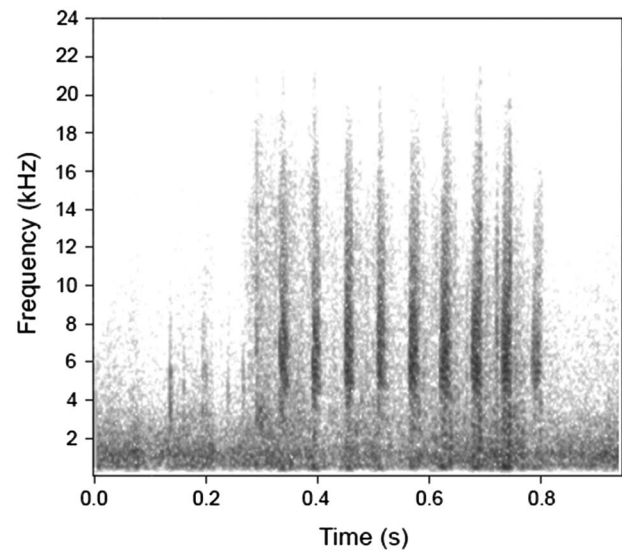


Fig. 2 Spectrogram of the takeoff flight of the scaled dove (*Columbina squammata*) in response to a potential risk

($\chi^2=4.60$; $P=0.031$; Fig. 3), but were not directly affected by the occurrence of a potential threat ($\chi^2=0.91$; $P=0.337$). The non-vocal sound produced by at least one of the flock members seems to positively affect the takeoff response of the other birds ($\chi^2=8.68$; $P=0.003$), but had no influence on the vigilance response immediately after the sound production ($\chi^2=0.01$; $P=0.909$). Flock members presented a faster response time (s) after the production of non-vocal sound ($\chi^2=80.30$; $P<0.001$; Fig. 4) in comparison to no sound production.

Part 2: Simulation of predation risk

We simulated predation attacks on 48 solitary individuals and 53 flocks (range 2–7). In all simulations, the target individual flew away from the area, being followed by at least

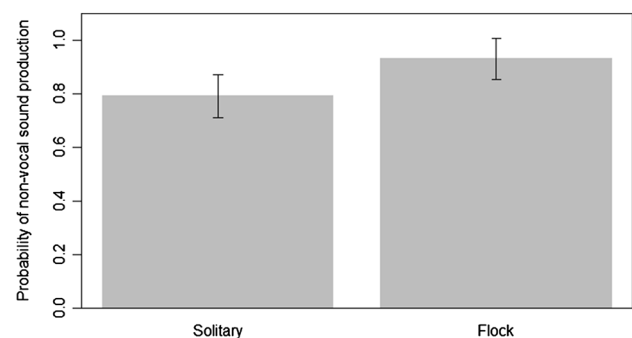


Fig. 3 Social organization (solitary vs. flock) effect on the non-vocal sound production (mean \pm SE) of the scaled dove (*Columbina squammata*) under natural context

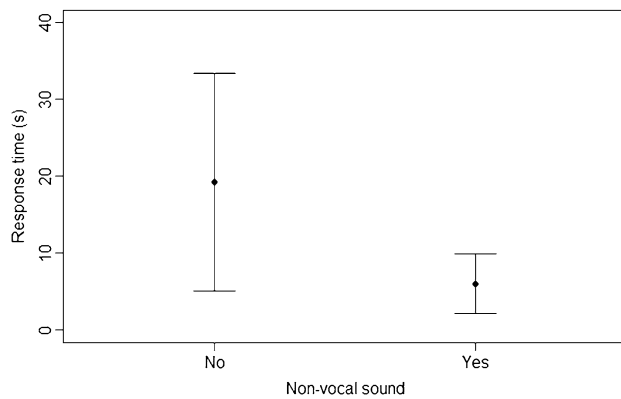


Fig. 4 Difference in the response time (s, 95% CI) associated or not with the production of the non-vocal sound by flock members of the scaled dove (*Columbina squammata*) under natural context

one member of the flock, in social conditions. Invariably, the target individuals produced the non-vocal sound during the escape takeoff. The alert response of flock members was determined by their position within the flock. Central individuals presented a higher probability to become vigilant after the production of the non-vocal sound than peripheral ones ($\chi^2 = 30.96$; $P < 0.001$; Fig. 5a). Similarly, central individuals were more likely to perform an escape takeoff after the non-vocal sound ($\chi^2 = 30.97$; $P < 0.001$; Fig. 5b). However, the response time of those central individuals was not faster than the ones in the periphery ($\chi^2 = 0.31$; $P = 0.576$).

Discussion

The production and function of mechanical sounds have been studied in several taxonomic groups including arthropods, mammals and birds. These non-vocal sounds were selected under different contexts and signal specific messages used during mate choice (Van Staaden and Römer 1997; Prum 1998; Bostwick and Prum 2003; Hebets 2008; Koch et al. 2015), territory defense (Miller and Inouye 1983; Bowen et al. 2008; Schuppe et al. 2016) and under perceived predation risk situations (Randall et al. 2000; Cristaldo et al. 2015). In some columbids, non-vocal sounds have been demonstrated to transmit relevant information about predation risk (Coleman 2008; Hingee and Magrath 2009; Murray et al. 2017). Here, we observed that the production of non-vocal sound during takeoffs is not mandatory in scaled doves. The results suggest that the non-vocal sound production may function mainly as a predation avoidance mechanism, but it is highly context-dependent. The non-vocal sound may have multiple signaling functions such as communicating information about predation risk and possibly group coordination (e.g., changing foraging area). This multiple signaling function on the same trait has been observed

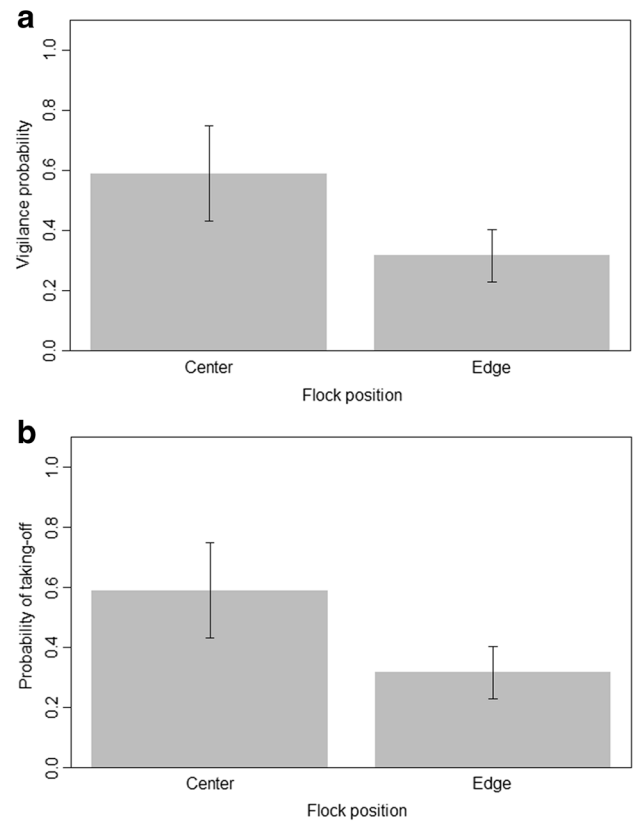


Fig. 5 **a** Effect of flock position on the vigilance state (mean \pm SE) of flock members of the scaled dove (*Columbina squammata*) and **b** effect of flock position on the probability of taking-off (mean \pm SE) by flock members of the scaled dove (*Columbina squammata*) after an experimental simulation of predation risk

for other species, such as the lined rainbow-skink (*Carlia jarnoldae*), which performs tail displays more frequently during competition with same-sex conspecifics and when interacting with potential predators (Langkilde et al. 2005).

In both natural and simulated contexts, potential threats seem to influence scaled dove escape decision. When a potential threat was present, all focal solitary individuals and at least one individual of each observed focal flocks fled. These results suggest that the perceived risk may differ between solitary and flocked birds, with solitary individuals responding promptly to any direct threat. A study that analyzed the effects of predatory threat on perches (*Perca fluviatilis*) demonstrated that solitary individuals were less bold than individuals in groups (Goldenberg et al. 2014). When evaluating the role of the non-vocal sound as an alarm information, we observed that, although the trill production was statistically more common in flocks, solitary individuals also produced non-vocal sound during escape takeoffs, especially under simulated attacks. This result indicates that trill production in scaled doves may have the function to warn conspecifics about a potential danger, but it might also

communicate to the predator that it has been spotted, as suggested for the wag-display of the turquoise-browed motmot (Murphy 2006). An investigation of acoustic directionality of antipredator calls from different bird species demonstrated that alarm calls usually have low directionality, suggesting that they function to communicate with surrounding conspecifics. However, some species can increase the directionality in the presence of predators, indicating that some antipredator calls are aimed at communicating with both conspecifics and predators (Yorzinski and Patricelli 2010). Warning conspecifics is the more common function of alarm signals (Burton and Yasukawa 2001; Dabelsteen 2005; Patricelli et al. 2008), but signals may carry other important information that could also influence predator decision (Curio 1978; Sherman 1985). For example, in Thomson's gazelles (*Gazella thomsoni*), it is likely that stotting serves to alert the predator that it has been detected (Caro 1986) or to advertise to the predator their escaping ability (Fitzgibbon and Fanshawe 1988). Alternatively, wing sound production may distract the predator, leaving time for individuals to escape, especially when the perceived danger is more intense (Sherman 1977).

In flocks of scaled doves, the production of the non-vocal sound during takeoffs elicited more escape responses in other flock members in comparison to takeoffs without sound production. Despite that, trill production did not affect the vigilance response of those individuals that chose to stay. The results suggest that some receivers interpret the non-vocal sound as a trigger to escape while others may incorporate different environment information about the potential risk of predation to formulate the decision whether to escape or stay. The risk sensitivity hypothesis predicts that several factors may influence prey response in encounters with predators (Lovegrove and Wissel 1988; Lovegrove 1991; Cooper 2009). This is because the risk varies as a function of the distance to the predator (Helfman 1989) in relation to group size (Helfman and Winkelman 2010) and may also be associated with cost reduction, such as avoid stopping foraging (Ydenberg and Dill 1986).

The escape response time was correlated with the production of the non-vocal sound. In natural conditions, individuals showed faster escape responses after the trill was produced. Variation in the speed of escape response may be associated with physical constraints related to signal detection or to the cost–benefit tradeoff of escaping (Ydenberg and Dill 1986; Quinn and Cresswell 2005). Possibly, the absence of other stimuli (e.g., a predator attack) may have made the escape decision less advantageous in some cases. Considering the context of non-vocal sound signaling, playback experiments on crested pigeons demonstrated that the mechanical wing whistle promoted an escape response in most analyzed flocks (Hingee and Magrath 2009). Additionally, wing whistle reproduced by zenaida doves (*Zenaidura*

aurita) increased vigilance of conspecifics, but seems to be less informative than the predator vocalization, suggesting that other clues from predators may influence predation risk perception (Barrera et al. 2011).

In the simulated attacks, central individuals presented a faster response after the wing trill production. Likewise, individuals in the center of the flock showed a higher probability to become vigilant after a potential threat, if they have not fled. Perceived predation risk and economic decisions may also explain the effect of the position within the flock on the escape response time and vigilance (Cooper, 2009; Quinn and Cresswell 2005). Movement coordination during escaping behavior is especially important to avoid collisions (Nudds and Bryant 2003; Usherwood et al. 2011) and to maximize the speed of response (Hilton et al. 1999). Here, due to the fact that the groups are small, loosely distributed and that the sound started at the edge of the flock, the faster speed of escape of central individuals could simply be due to their, on average, closer spatial distance in relation to the non-vocal sound source (but see Beauchamp 2012).

In addition to its anti-predator properties, non-vocal sound production may be relevant for group coordination in order to maintain group cohesion (Conradt and Roper 2003). Individuals may use the mechanical sound to inform other group members that they are leaving the area. The timing and directionality of group movement are relevant to avoid reducing the benefits of group living (Krause and Ruxton 2002; Conradt and Roper 2007). Factors other than a predator attack (e.g., food depletion) may be responsible for initiating the movement of some individuals of the flock. Groups of meerkats (*Suricata suricatta*), for example, use individual calls as an assessment of food patch quality to decide whether or not to move (Bousquet et al. 2011).

Predation is one of the main forces shaping the evolution of survival strategies. Despite being a potential source of information, there is little evidence about the use of non-vocal sounds to alert concerning predation risk. The effects of the non-vocal sound production on the behavior of aggregated conspecifics, and the suggestion, still to be confirmed, of a voluntary sound production, weaken the possibility that the non-vocal sound is merely a non-intentional cue. Under an evolutionary perspective, it is probable that the non-vocal sound production must have become an important source of information through its accumulated benefits acquired by social individuals and its dissuasive potential, considering its possible effects on predators. Here, we suggest that the mechanical sound produced by scaled doves during escape takeoffs might be used for intraspecific communication about predation risk and during predator–prey interactions. Future manipulations based on feather removal and playback experiments may help to clarify some of the gaps not addressed in this study. Several questions are still open for future studies such as (1) how does the mechanism

of sound production work in scaled doves? (2) Do non-vocal sound characteristics (e.g., sound amplitude) influence group members' response? And (3) what is the effect of the non-vocal sound on predator behavior? In addition, much more research is still needed to help elucidate the role of non-vocal communication in birds.

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Compliance with ethical standards

Conflict of interest P S. Amorim and R. I. Dias declare that they have no conflicts of interest.

Ethical statement All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. The study complied with the current laws of Brazil under permit 50793 from Instituto Brasileiro de Recursos Renováveis (IBAMA).

Human participants This article does not contain any studies with human participants performed by any of the authors.

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