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ORIGINAL ARTICLE

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Does information of predators influence general wariness?

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Abstract Antipredator behavior includes several qualitatively distinct activities, but few studies have determined the degree to which these activities are independent. If behaviors are not independent, then the nature of the relationship would illustrate potential performance constraints. We studied crimson rosellas (*Platycercus elegans*) and first focused on acoustic predator discrimination. We measured time allocation before and after playback of one of three experimental treatments (peregrine falcons—*Falco peregrinus*, wedge-tailed eagles—*Aquila audax*, and crimson rosellas) to determine whether or not rosellas discriminated predators from non-predators, and specifically whether or not they discriminated large from small predators. We then focused on the decision to flee. We experimentally approached subjects and measured the distance at which they oriented to us (alert distance) and the distance at which they fled (flight initiation distance; FID). We found that rosellas could distinguish among predators; however, there was no effect on general wariness as measured by FID. These two processes of antipredator behavior may, thus, be independent.

Keywords Antipredator behavior · Crimson rosellas · Flight initiation distance · Predator recognition

Introduction

Many species respond to the vocalizations of their predators (e.g., birds; Hauser and Caffrey 1994; Rainey et al. 2004; mammals; Swaisgood et al. 1999; Gil-da-Costa et al. 2003) and identifying predators and modifying one's assessment of risk is an important mechanism by which individuals reduce the risk of predation (Lima and Dill 1990; Caro 2005). Responses to predator vocalizations may involve both immediate reactions, as well as behavioral changes over variable time scales. For instance, distinct antipredator responses of mantled howler monkeys (*Alouatta palliata*) in Panama were observed after playbacks of calls made by harpy eagles (*Harpia harpyja*) (Gil-da-Costa et al. 2003), while nesting pied flycatchers (*Ficedula hypoleuca*) changed nest visitation rates in response to the playback of a pygmy owl (*Glaucidium passerinum*) whistling call (Hakkarainen et al. 2002).

Predator recognition is one of a series of activities that prey can do to avoid predation (Lima and Dill 1990; Caro 2005). While there is evidence that vocalizations of predators may change prey behavior on various time scales, we do not know if identifying a predator necessarily has consequences for other types of antipredator behavior. Specifically, we do not know if identifying the presence of an aerial predator might influence subsequent responses to terrestrial predators, or if these different stages of predation hazard assessment and management function independently.

Prey may alter their behavior as they assess risk according to the perceived threat of predation (Lima and Dill 1990; Cooper 1997). Thus, we might expect an increase in general flightiness of prey after playback of a predator vocalization. General flightiness should be expected to vary because fleeing non-threatening predators wastes time and energy, while not fleeing in response to a threat could result in death (Blumstein 2003; Deeke et al. 2002; Lank and Ydenberg 2003). The ability to differentiate and assess variable degrees of risk based on the presence of various species of raptors has been observed in black-capped chickadees (*Poecile atricapilla*) (Templeton et al. 2005). Discriminating between variable levels of risk would benefit prey by helping them avoid death while maximizing time allocated to productive behaviors.

Smaller birds have a larger power-to-mass ratio than larger birds, thus allowing them to accelerate more rapidly, which allows for greater escape performance (Dial 2003).

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The escape performance of a small, agile bird can be expected to influence its assessment of risk, as the physical capability to outmaneuver a predator decreases the likelihood that it will be caught. Because flight performance in birds declines as body size increases (Tobalske and Dial 2000), prey should be most vulnerable to relatively smaller raptors rather than larger ones.

We focused on crimson rosellas and their response to playbacks of two raptors of relatively different sizes (peregrine falcons and wedge-tailed eagles), as well as to playbacks of conspecifics. Peregrine falcons are reported to eat mostly birds, including rosellas and other parrots (Stubbs 1996; Olsen et al. 2004), while wedge-tailed eagles are known to eat birds during breeding season (Harder 2000; Sharp et al. 2002). If crimson rosellas discriminated among their predators, then playbacks with vocalizations of the smaller-sized peregrine falcon should elicit a greater response when compared with the playback of vocalizations of the larger, and thus less-threatening, wedge-tailed eagle.

If the calls of various sized raptors created different perceptions of risk, then we expected to see differences in vigilance in response to playback. We wished to determine if this immediate response also increased general wariness. To quantify vigilance, we conducted focal animal samples, and to quantify general wariness, we measured flight initiation distance. Flight initiation distance (FID) is the distance to which a perceived threat can approach a target prey before an escape response is elicited (Blumstein 2003). The decision to flee is contingent upon various opportunity costs (Ydenberg and Dill 1986). Thus, animals should minimize the cost of missed opportunities by prolonging escape response until the risk of mortality exceeds the cost of remaining (Ydenberg and Dill 1986). If an individual's assessment of risk varied, we then expected that FID would also vary. Specifically, we expected animals that heard high-risk peregrine falcon calls to initiate flight at greater distances than those hearing control sounds.

Materials and methods

Study site

The study was conducted in and around Booderee National Park (34°58′ S, 150°41′ E), Australian Capital Territory, from 19 October to 1 November 2005. Crimson rosellas are a mid-sized parrot, often found in pairs of family groups, that feeds in the foliage as well as at the edge of clearings (Pizzey 1980). Rosellas were found in a variety of habitat types in the park, but the majority of our experiments were conducted on rosellas that were foraging or preening in coastal tea trees (*Leptospermum laevigatum*), which themselves were found in a variety of habitat types. Experiments were primarily carried out between 0600 and 1000 hours, Australian eastern standard time. Crimson rosellas were most active between 0730 and 0900 hours. To minimize the potential re-sampling of study subjects, we worked at a variety of sites and did not re-visit locations where we conducted experiments.

Focal protocol

We focused on relaxed crimson rosellas who were either foraging or preening and at which we had a direct line of sight and approach (i.e., so that we did not have to later walk through heavy undergrowth while approaching subjects). All but eight of our subjects were in trees; the eight that were on the ground were within 2 m of the nearest cover (there was no systematic bias as a function of subsequent playback stimulus: two of the rosellas on the ground were broadcast the falcons, three rosellas on the ground were broadcast the rosellas, and three of the rosellas on the ground were broadcast the eagles.

We conducted a 60-s focal animal observation (Martin and Bateson 1986) that was divided into two 30-s periods; a 30-s baseline period during which we observed a subject before playback, immediately followed by a 30-s period that included the 10-s playback. Our ethogram included the following behaviors: look (scored with each quick turn of a test subject's head, while test subject's posture was upright), call (emitting one of several vocalizations), forage (feeding with head down), preen (contact of beak with body parts, e.g., wings and feet), walk (forward movement greater than two steps), hop (in air without wing movement), fly (in air with wing movement), out of sight, and others.

We calculated the difference from baseline behaviors as our measure of responsiveness and plotted all of these results. As metrics of vigilance, we focused on the number of looks and the time allocated to looking in our statistical analyses. We considered foraging and preening to reflect relaxed behaviors; they were not used to measure vigilance. Walking, hopping, calling, and flying occasionally occurred immediately after playback, but they were infrequent and, while initially scored, they were not analyzed further. A single observer recorded these observations onto a cassette recorder and then later quantified time allocation using JWatcher (version 1.0; Blumstein et al. 2006).

Playback protocol

Vocalizations were compiled from the Internet (http://www.mangoverde.com) and commercial cassettes (Buckingham and Jackson 1985), digitized at 16 bit, 44 kHz, edited and normalized to 95% of peak amplitude with Sound Edit 16 (version 2, Macromedia 1996), and then uploaded to a Generation 4 iPod (Apple Computer, Cupertino, CA, USA). Calls were broadcast through a powered speaker (Pignose 7-100-R, Pignose Industries, Las Vegas, NV, USA) at 92–98 dB SPL measured 1 m from the speaker with a digital sound meter (SPER Scientific 840029). The speaker averaged 26.0 m (±9.9 SD) from the focal subject.

After 30 s of pre-playback observation, one of three experimental treatments was randomly applied. The first, control treatment, was comprised of three exemplars of crimson rosella contact calls. We elected to use rosella contact calls because rosellas regularly heard these calls and their presence should not indicate a heightened risk of predation, nor a threat from a possible foraging competitor (we commonly observed rosellas displaced by other local parrot species such as rainbow lorikeets (*Trichoglossus haematodus)* and sulfur-crested cockatoos (*Cacatua galerita*). Thus, we used the rosella calls to represent a low-risk situation. The second treatment consisted of three exemplars of peregrine falcon vocalizations, representing the smaller, more agile avian predator. The third treatment consisted of three exemplars of wedge-tailed eagle vocalizations, representing the larger avian predator. Treatments were broadcast two consecutive times per subject for a total of 10 s. Our sample consisted of 47 observations: 18 peregrine, 16 rosella, and 15 wedge-tailed eagle.

Calculating flight initiation distance

Thirty seconds after the start of the playback (i.e., after 60 s of focal observation), a researcher approached the study subject, walking at a constant pace of approximately 0.5 m/s. Starting distance (the distance from the focal subject at the start of the experimental approach), alert distance—AD—(the distance from the focal subject when it oriented towards the approaching person), and FID (the distance to the subject when it initiated flight) were measured in paces and converted to meters. For crimson rosellas that were already in motion (e.g., those walking slowly and foraging), we scored flight initiation when a subject initiated a discernible departure behavior, such as hopping to a more distant location or actual flight (Blumstein et al. 2004). As we could not always detect alert distance, the final sample sizes for this experiment were *n*=13 for the peregrine, *n*=14 for the rosella, and *n*=16 for the wedge-tailed eagle.

We determined the $\mathrm{FID_{direct}}$ (the distance from the observer to the test subject at flush) by using the formula $[\mathrm{FID_{direct}}=\sqrt{(\mathrm{FID^2_{horizontal}}+\text{perching height}^2)}]$. $\mathrm{FID_{horizontal}}$ is the ground distance from the observer at the moment of flush to the point directly below the test subject at flush. We measured the perching height of the subject by visually rotating this distance to a horizontal position onto the ground, and then measuring the linear distance on the ground (Blumstein et al. 2004).

Statistical analyses

We compared both responses to predator vs rosella calls, as well as the specific responses to each stimulus. We compared the difference from baseline in the number of looks and the proportion of time allocated to looking in response to a predator call vs a rosella call using *t* tests and we used ANOVA to quantify the response to the three different treatments. We fitted a general linear model to test the effect of prior exposure to a playback stimulus on the relationship between alert distance (AD) and FID. Following Cárdenas et al. (2005), our models had no intercepts because an alert distance of 0 m would logically have an FID of 0 m, and we tested the effect of the categorical factor on the expected relationship between AD and FID (e.g., Blumstein 2003; Blumstein et al. 2005; Cárdenas et al. 2005) by testing its interaction with AD. We did this because these were calculated for both the predator vs non-predator categories, as well as the three treatments separately. We also fitted a MANOVA to test whether the mean AD and FID response was influenced by treatment (again, calculated for both the predator vs non-predator categories, as well as the three treatments separately).

We fitted models using SPSS 11.0 for the Macintosh (SPSS, Chicago, IL, USA). We reported the mean, standard deviation, and sample size for results. We interpreted significance when $\alpha<0.05$ and use partial η^2 as a measure of the effect size of the independent variables on our model. In all cases, variances across treatments were homogeneous and residuals were normally distributed.

Results

Can crimson rosellas discriminate predators acoustically?

Before playback, there were no significant differences in the number of looking bouts whether split by rosella/predator (t=1.186, df=45, p=0.242), or by the specific type of stimulus (F=1.339, df=2, 44,p= 0.273). Rosellas looked an average of 4.85 (±4.79 SD) times/30 s. Nor was there any difference in the proportion time allocated to looking whether split by rosella/predator (t=−1.088, df=45, p=0.282), or by the specific type of stimulus (F=0.830, df=2, 44, p=0.443). Rosellas allocated an average of 0.32 (±0.32) of their time to looking.

Playback stimulus had a significant effect on crimson rosella time allocation. The average (±SD) change in the number of looks in response to predator playback (2.10± 4.43, n=31) was significantly (t=−2.678, df=45, p=0.010) greater than that after control playback (−1.50±4.23, n=16, Fig. 1).

There was no significant (t=−1.660, df=45, p=0.104) effect of playback on the time allocated to looking (Fig. 1). We also found no significant (F=0.030, df=2, 44, p=0.187) differences when we looked at the specific stimuli (Fig. 2). Thus, while rosellas moved their head more after playback than before playback, they did not change the amount of time allocated to looking.

Additionally, we found a significant effect of the specific stimulus on the change in the number of looks (Fig. 2). The overall model was significant (F=3.784, df=2, 44, p=0.030) and post-hoc analyses demonstrated that peregrine falcons elicited significantly different responses than crimson rosellas (mean difference=−4.13, p=0.011), but we found no effect of wedge-tailed eagles eliciting different responses from other stimuli. In summary, crimson rosellas moved their head more after predator playbacks (particularly after peregrine falcon playback) than before predator playbacks, but did not change the amount of time allocated to looking.

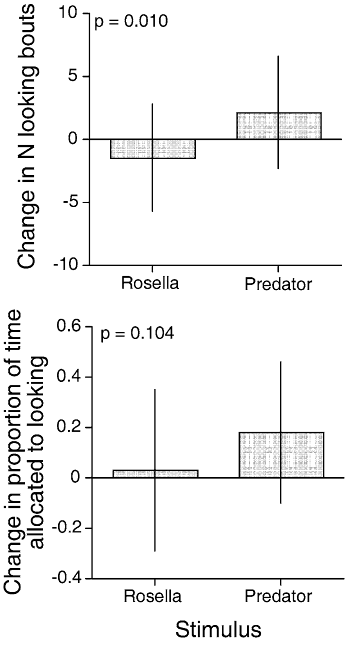

Fig. 1 Mean(±SD) difference in pre- and post-playback number of looking bouts (*top*) and difference in pre- and post-playback proportion of time in sight spent looking (*bottom*) as a function of playback stimulus (rosella/predator)

Does hearing a predator influence the decision to flee?

We found no effect of prior exposure to vocalizations on the relationship between alert distance and FID. For the two-treatment analysis: predator vs non-predator, 78% of the variance in FID was explained by alert distance, but no significant (partial η^2=0.019, p=0.375) variance was explained by the interaction of alert distance and FID (Fig. 3). 78.3% of the variance in FID was explained by alert distance and FID for the three-treatment analysis, but again no significant variation (partial η^2=0.059, p=0.298) was explained by the interaction of alert distance and FID (Fig. 3).

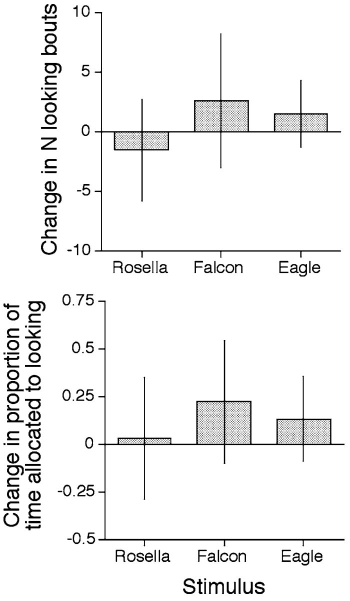

Fig. 2 Mean (±SD) difference in pre- and post-playback number of looking bouts (*top*) and difference in pre- and post-playback proportion of time in sight spent looking (*bottom*) as a function of specific playback stimulus (rosella/falcon/eagle)

MANOVA results paralleled GLM results suggesting that treatment had no effect on the average AD or FID. There was no difference in escape decisions in response to hearing the three stimuli (Wilk's Lambda=0.927, F=0.696, df=4, 72, p=0.597, partial η^2=0.037), or when comparing the response to hearing predators vs rosellas (Wilk's Lambda=0.992, F=0.144, df=2, 37, p=0.867, partial η^2=0.008).

Discussion

Recently, it was suggested that many, but not all, species studied respond to the vocalizations of their predators (Blumstein et al. unpublished data). Our results showed that crimson rosellas react to playback calls of their potential avian predators by increasing the number of looks after playback, while not significantly altering baseline behavior in response to the calls of conspecifics. This discrimination between predatory and non-predatory acoustic signals suggests that the raptor calls were recognized as a potential threat, which resulted in increased vigilance.

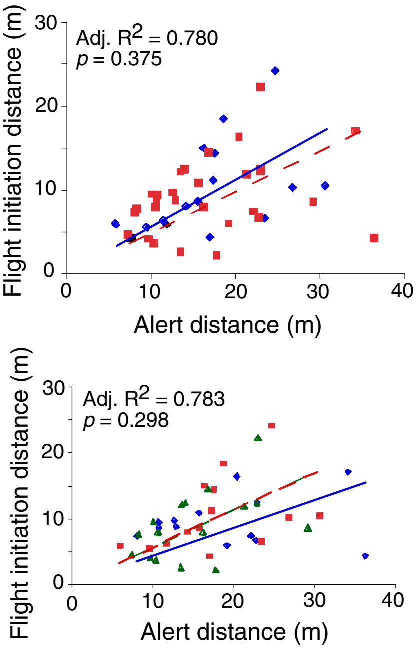

Fig. 3 The relationship between alert distance and flight initiation distance for crimson rosellas approached by a human following the experimental playback of predator or non-predator vocalizations. The *top graph* illustrates the effect of hearing either a peregrine falcon or a wedge-tailed eagle (*square*, *dashed line*) or a non-predatory rosella call (*diamond*, *solid line*). The lower graph illustrates the effect of each of the three stimulus categories on response: rosella—*square*, *dashed line*; wedge-tailed eagle—*triangle*, *dashed line*; peregrine—*diamond*, *solid line*

Geoffroy's marmosets (*Callithrix geoffroyi*) increased vigilance after playback of calls from an avian predator, but did not alter behavior after playback calls of non-threatening animals (Searcy and Caine 2003). However, the marmosets fled immediately to protected areas where they would often resume baseline rates of behavior, whereas the rosellas we studied did not immediately flee. Similarly, Fichtel and Kappeler (2002) found that individuals of two lemur species were able to discriminate among predator vocalizations when individuals were initially in cover. Almost all of our rosellas were already within cover at the start of our observations, and those foraging on the ground typically flew to the nearest cover if an alarming stimulus was played, which was never more than 2 m away. This indicates that rosellas were taking preemptive measures by staying close to the nearest refuge and initiating their escape accordingly (Lima and Dill 1990).

Interestingly, rosellas showed a greater response to a potentially more threatening predator (peregrine falcon) than to a potentially less threatening predator (wedge-tailed eagle). This ability to discriminate calls from two raptors of very different flight capabilities mirrors the recent study of black-capped chickadees, which altered their alarm calls based on the relative threat of a raptor (Templeton et al. 2005). Accordingly, the call of a peregrine falcon should elicit a greater number of looks because Falconidae exhibit versatile flight capabilities with their long wing span to body size ratio, thus they are a formidable predator (Dial 2003). Discrimination amongst avian predators has also been observed in chickens (*Gallus gallus*), which vary their antipredator response according to visual cues and the size of the perceived risk (Palleroni et al. 2005).

The importance of discriminating among avian predators is potentially important. Falcons are notorious for catching small- to medium-sized birds on the wing (Grossman and Hamlet 1988). Thus, fleeing a falcon is relatively risky. Wedge-tailed eagles, however, employ a different hunting technique that requires less maneuverability and more strength to tackle large prey, such as wallabies (Grossman and Hamlet 1988). Therefore, hearing a wedge-tailed eagle does not pose a great threat to the much more swift and nimble rosella who, if in cover, is relatively safe from eagle predation.

Despite an increased number of looks after the playback of calls from potential predators, rosellas did not increase the amount of time allocated to looking after playback. One possible explanation is that many predators employ an ambush technique of hunting, therefore making a greater amount of time allocated to looking a waste of time and energy to the rosella. However, it has been shown that large birds of prey such as harpy eagles do vocalize before attacking prey (Gil-da-Costa et al. 2003). Thus, it seems that rather than increasing time allocated to vigilance, alarmed rosellas simply increase the rate at which they scan their environment. Though rosellas had the ability to discriminate predators from conspecifics by hearing their vocalizations, we found no evidence that this affected general wariness; we found no effect of treatment on the relationship between alert distance and FID. There are at least three possible interpretations that may explain the discontinuity between increased vigilance and the decision to flee.

First, it is possible that the rosellas were already aware of the oncoming threat but that we were unable to detect this. An animal's ability to detect danger with its head down has been shown to affect vigilance and other subsequent antipredatory behaviors (Lima and Bednekoff 1999). If so, this suggests that the rosellas were able to be vigilant when not overtly so, thereby affecting the measured alert distance and subsequent FID. We find this unlikely because we found that alert distance explained virtually all of the variation in FID. This suggests that the rosellas did, in fact, become alert when they oriented to us.

Second, the rosellas may have in fact been alert, but focused their attention to the sky for an anticipated aerial predator. Some birds use lower field myopia to keep objects on the ground in focus, while simultaneously scanning the air for predators (Hodos and Erichsen 1990). Therefore, it is possible that the rosellas used this visual adaptation to maintain their position for foraging, and did not change their assessment of risk due to the ability to recognize the researcher as the potential threat. We find this unlikely because the playback of rosella calls did not elicit a significantly different FID response than predator calls.

Third, the rosellas sampled in Booderee National Park were in the middle of nesting season, and decisions to flee in the presence of danger could have been influenced by the bird's proximity to its nest or young. Crimson rosellas defend a buffer zone in areas surrounding their nest cavity even before eggs are present because there are often insufficient nesting holes (Krebs 1998). These defensive behaviors may carry over to situations when eggs and young are present and most likely affect the rosellas assessment of risk when it comes to fleeing. Domestic hens have also been shown to vary their antipredator responses according to predator body size by actually attacking smaller raptors when newly hatched young were present (Palleroni et al. 2005). Further experiments at other times of the year would be required to properly refute this hypothesis.

We, therefore, conclude that while crimson rosellas do discriminate between aerial predators, knowledge of the presence of an aerial predator does not affect the response to an approaching terrestrial predator as we measured it. Thus, it appears that rosella antipredator behaviors are not necessarily linked. The plasticity in behavioral decisions made after playback of a potential predator suggests that rosellas may optimize each part of their multi-stage response. Rosellas may be relatively safe from potential predators when foraging in trees. While not possible with rosellas, it would be informative to broadcast both terrestrial and aerial calls to ground-dwelling birds such as galliforms and see if this influences their FID. If not, we would be in a better position to conclude that the decision to flee is not influenced by specific acoustics threats.

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