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Effect of visibility on time allocation and escape decisions in crimson rosellas

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Abstract. Most studies of antipredator behaviour have focused on a single behaviour at a time, but ubiquitous factors may simultaneously influence a variety of activities. Habitat structure influences visibility, which influences both the ability of prey to detect and respond to their predators. We studied how habitat visibility influenced time allocation and escape decisions of crimson rosellas (*Playcercus elegans*). We examined the effect of visibility on time allocated to looking, locomotion and foraging. We measured escape decisions by experimentally approaching rosellas until they fled. We measured visibility by standing 12 m away from a 1-m^2 white sheet containing 36 points and counting the number of points that were visible. As measured, visibility influenced time allocated to both foraging and locomotion. However, there was no effect of visibility on flight-initiation distance or two other related measures of escape (a measure of the latency to detect an approaching threat or the latency to flee once the threat was detected). Therefore, crimson rosellas modified their behaviour as a function of visibility, but this did not influence their decision to flee from an approaching human. We infer that they are sensitive to variation in visibility, but that this does not influence their overall perception of risk as we measured it. These two stages of antipredator behaviour may thus be largely independent; ubiquitous factors need not have ubiquitous effects on different aspects of antipredator behaviour.

Introduction

Avoiding predation is a multistep process, and selection should act at every step (Lima and Dill 1990). From the prey's perspective, protecting oneself from predation may include having certain morphological traits, being able to recognise predators, possessing a variety of individual behavioural strategies to reduce predation risk, engaging in group defenses, and making decisions about when and how to flee (Lima and Dill 1990; Caro 2005). While most studies focus on a single aspect of antipredator behaviour at a time (Caro 2005), these multiple stages of antipredator defence may be influenced by certain ubiquitous factors and, if so, they may not be independent of each other. Knowledge of the influence of these factors on predation risk and its subsequent effect on the expression of antipredator behaviour is limited, but identifying the effect of such factors is important because it may highlight constraints on adaptive responses. Habitat structure is a ubiquitous factor that may affect time allocation and escape decisions because habitat influences visibility and thus can influence overall predation risk. Habitat structure and the resulting visibility thus may influence multiple stages of antipredator behaviour.

Habitat structure can be considered obstructive or protective (Finne *et al*. 2000; Whittingham and Evans 2004). If the habitat structure is obstructive, the individual's ability to detect predators is limited by the visibility. For instance, Arnez and Leger (1997) found that peripheral visibility influenced foraging bout length of squirrels. If habitat structure is considered protective, the individual is able to seek refuge from the predator based on the amount of surrounding foliage, or may be less conspicuous when in cover (Cooper 2003). Lima (1992) suggested that birds behaved in ways consistent with the hypothesis that they assessed lower risk in trees with larger trunks and less visibility. Regardless of whether cover is protective or obstructive, foliage density has been shown to influence time allocated to vigilance in birds (Metcalfe 1984; Whittingham *et al*. 2004), and flight decisions in lizards (Martin and López 1995), mammals (Blumstein *et al*. 2004*b*) and birds (Fernández-Juricic *et al*. 2002, 2004).

Flight-initiation distance is the distance from a predator at which an individual initiates its escape, and alert distance is the distance from a predator that an individual orients towards the approaching predator. Flight-initiation distance (Stankowich and Blumstein 2005), and the relationship between alert distance and flight-initiation distance (Blumstein *et al*. 2005*b*), are often used to quantify wariness in animals and to identify factors that influence wariness.

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Our study focused on time allocation and escape decisions of crimson rosellas in habitats with varying degrees of visibility. We measured habitat visibility by standing 12 m away from a 1-m^2 white sheet containing 36 points and counting the number of points that were visible. We analysed time allocated to looking, foraging, and locomotion using 2-min focal animal samples (Martin and Bateson 1993). Escape decisions were measured by experimentally approaching rosellas until they fled. We assumed that if rosellas perceived cover as obstructing their field of view and their ability to detect approaching predators, (1) rosellas should be more vigilant and forage less, and (2) that if this is the case, they may be slower to detect an approaching predator and hence flight-initiation distance would decrease.

Methods

Study site and target species

Between 20 and 31 October 2005, we studied the crimson rosella, a mid-sized parrot, in and around Booderee National Park, Australian Capital Territory. This species was commonly found foraging on the ground or in tea trees (*Leptospermum* sp.). During the breeding season, we found them typically in groups of 1–3 individuals and usually studied solitary subjects. Additionally, birds were found perched in or flying through *Eucalyptus* spp. Importantly, the rosellas were found in areas of varied visibility. Most of the park is characterised as eucalypt forest, dominated by *E. pilularis* and *E. botryoides*, much of which was recovering from a widespread bushfire during 2003. We capitalised on this fire for our study because it created a variety of habitat visibilities throughout the park.

Visibility

Habitat visibility was measured for each trial using a 1-m^2 white sheet draped on a 1-m^2 polyvinyl chloride frame. The sheet contained 36 black dots with a radius of 1 cm, evenly spaced 15 cm from each other. Birds were found between 0 m and 9.33 m high (mean = 3.53, s.d. = 2.71). The frame was held at chest height where we saw the target bird and faced an observer 12 m away. The number of dots that the observer could see was recorded. Four visibility measurements were recorded for each trial. The first visibility measurement was taken in the line of sight between the location of the target bird and the location of the initial observation of the target bird. The subsequent three visibility measurements were taken every 90° around the location of the target bird. The four visibility measurements were averaged and an index visibility was calculated by dividing by the total number of dots on the sheet. We acknowledge that this reflects only a general index of visibility in the habitat, and not the visibility from the birds' perspective at the time of data collection. While not specifically quantified, dense habitats generally had low visibility throughout them, while more open habitats typically had greater visibility throughout them. Because predators may come from any direction, we believe that this is a suitable metric of habitat-related visibility. Moreover, we found significant effects of visibility on time allocation, a finding consistent with the hypothesis that this measure of visibility is salient to the birds.

Does visibility influence time allocation?

In order to find subjects we walked through the national park on footpaths, fire service roads, and paved roads. When a rosella was spotted, we recorded focal behaviour into a microcassette recorder for 2 min. Our ethogram contained the following behaviours: looking (head elevated, each move of the head was counted as a new look), foraging (actively manipulating food with beak), walking, hopping, flying, calling, out of sight, and other. Focal animal samples were scored using JWatcher 1.0 β (Blumstein *et al.* 2005*a*) to obtain the discrete number of occurrences of each behaviour, and the proportion of time that the bird exhibited each behaviour. In addition, the bird's position (on the ground or in a tree) was recorded, and visibility was measured.

For analysis, walking, hopping, and flying were grouped into a category, 'total locomotion'. We regressed visibility against the number of events and our estimates of time allocation. Because we conducted three analyses, we controlled for Type I error rate using a Rice Correction (Rice 1989).

Does visibility influence flight-initiation distance?

On another occasion, we experimentally approached subjects. Humans are routinely used as an alarming stimuli in studies of predation hazard assessment (e.g. Blumstein 2003; Cooper 2003; Fernández-Juricic *et al.* 2004). Importantly, rosellas have traditionally been eaten by people (Olsen 2006), and rosellas are viewed as agricultural pests and are harassed in many places in their range (http://www.birdgard.com.au, accessed September 2006). When a target rosella was spotted, the observer dropped a 'starting distance' marker and started walking towards the bird in a straight line at a rate of 0.5 m s^{-1}. An 'alert distance' marker was dropped when the bird oriented towards us. When the bird initiated flight, a 'flight-initiation distance' marker was dropped. Bird position was noted before the experimental approach. If the bird was perched in a tree, its distance from the ground was measured by visually rotating the location of the bird in the tree onto the ground and then measuring this linear distance on the ground (e.g. Blumstein *et al.* 2004*a*). Distances on ground were measured in paces by the observer and later converted to metres. Finally, visibility was measured at, or directly under, the original position of the bird.

Blumstein *et al.* (2004*a*) found that crimson rosellas flushed at a greater distance when more than 3 m high in a tree than when below 3 m. Therefore, height is important in escape decisions, and the direct flight-initiation distance must be used. Horizontal flight-initiation distance and perching height was converted subsequently into direct flight-initiation distances using the Pythagorean Theorem.

We studied the effect of visibility on flight-initiation distance in two ways. First, we examined the effect of visibility on the relationship between alert distance and flight-initiation distance by fitting a general linear model in SPSS 11 (SPSS 2002). We used the flight-initiation distance as the dependent variable. Independent variables included the main effects of alert distance and visibility and the interaction between alert distance and visibility. Following Blumstein (2003), this model had no intercepts because flight-initiation distance has to be 0 m when an alert distance is 0 m. Second, we used linear regressions to examine the effect of visibility on the difference between starting distance and alert distance (a measure of the detection delay) and on the difference between alert distance and flight-initiation distance (a measure of post-detection delay).

In all cases, significance was inferred when *P*-values were less than 0.05. We used partial η^2 values and adjusted R^2 values to infer the relative importance of the terms and the models. We checked residuals from linear models for normality and found that no transformations were necessary.

Results

Does visibility affect time allocation?

Analysis of focal animal samples ($N = 28$) demonstrated that visibility significantly explained variation in the number of foraging bouts (adjusted R^2 = 0.204, P = 0.009) and the number of locomotion bouts (adjusted $R^2 = 0.272, P = 0.003$) (Fig. 1). After adjusting for multiple comparisons, no other behaviours were significantly influenced by visibility as we measured it (Fig. 1).

Does visibility influence flight-initiation distance?

Of the 41 experimental approaches, starting distances ranged from 3.5 to 56 m, while visibility ranged from 0.18 to 1. The model explained 85.3% of the variation in flight-initiation distance. Alert distance significantly ($P < 0.001$) explained 49.3% of the total variation. We found no significant main effect of visibility (partial $\eta^2 = 0.026$, $P = 0.315$) or the interaction between alert distance and visibility (partial $\eta^2 = 0.052$, $P = 0.157$). There was no relationship between visibility and the latency to detect an approaching threat (adjusted $R^2 = 0$, $P = 0.963$), nor was there a relationship between the latency to respond, once a threat was detected (adjusted $R^2 = 0.01$, $P = 0.253$). Thus, any way we examined

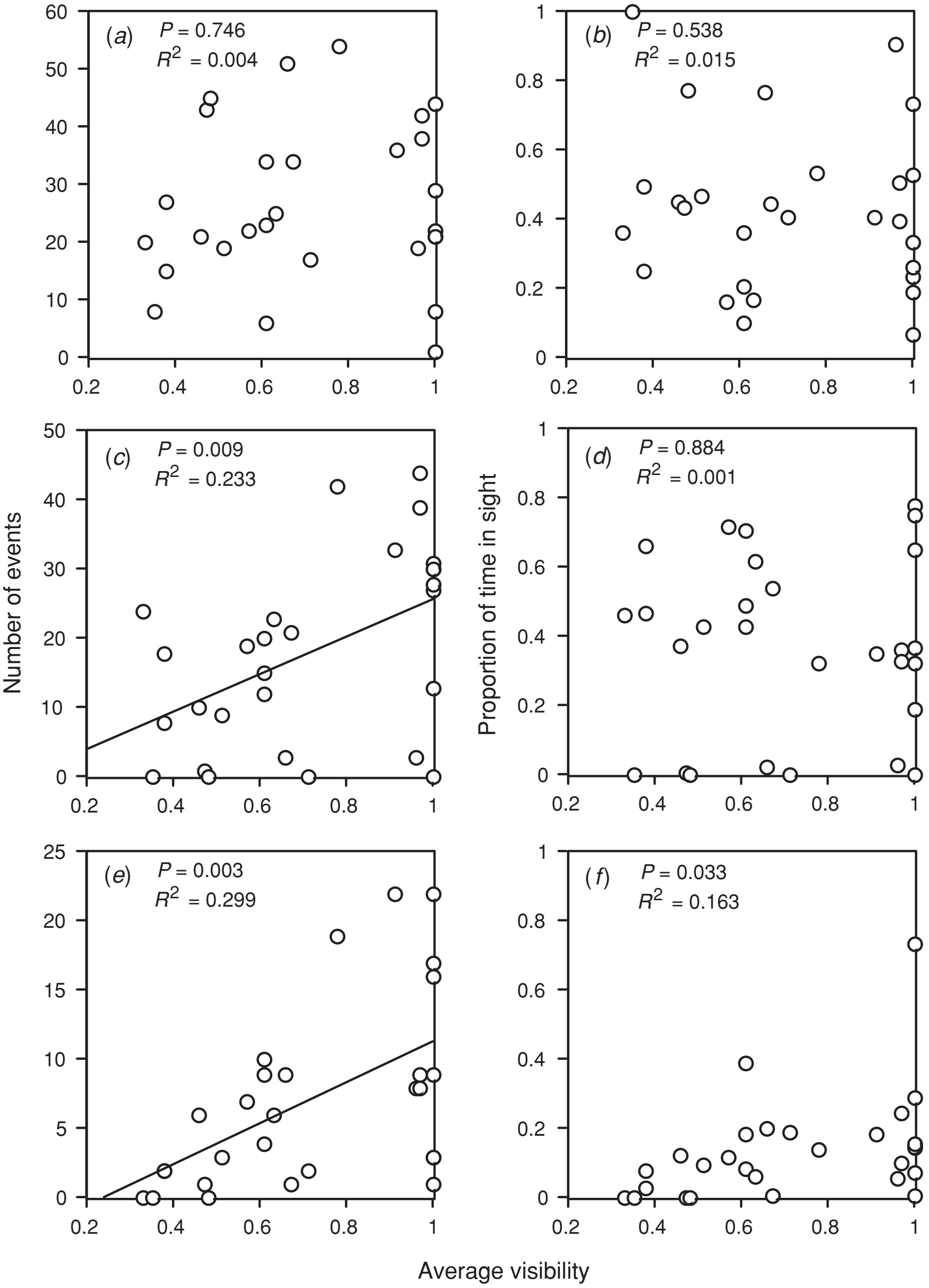

Fig. 1. The relationship between average visibility and number of events and proportion of time in sight allocated looking (*a*, *b*), foraging (*c*, *d*) and locomotion (*e*, *f*). Regressions that are significant after the Rice correction are illustrated with regression lines.

it, visibility explained no variation in the response of rosellas to an approaching threat.

Discussion

While previous single-species studies have reported habitat-specific effects on flight responses in birds (Fernández-Juricic *et al*. 2002), a comparative analysis of 150 species found no systematic effect of habitat type on flight responses in birds (Blumstein 2006). We are aware of no previous study of birds that specifically measured the visibility in the area where individuals were experimentally approached. Our study of crimson rosellas found that they modified their foraging behaviour as a function of visibility, but variation in visibility did not influence their decision to flee from an approaching human. Our study specifically focused on an attribute of visibility that was salient to the rosellas. Thus, finding an extremely small effect of the alert distance by visibility interaction, combined with a lack of significant relationships between visibility and measures of detection responses or postdetection responses, allows us to conclude that while rosellas are sensitive to variation in visibility, this does not influence flight decisions.

Our result, that rosellas foraged more in areas with high visibility, could mean that they viewed cover as obstructive, and thus felt safer in the open. Based on our other observations, this seems unlikely because we found no significant reduction in vigilance in more visible areas. Conversely, Blumstein *et al*. (2004*b*) found that some birds may actually forage more in locations or situations where they feel less safe because they want to minimise exposure in open habitats and spend as little time as possible in them. This could explain the observation that foraging events increased as visibility increased, but that time allocated to vigilance did not increase.

Visibility as we measured it did not, however, influence escape decisions. To experimentally approach a subject, we required a clear line of sight. Thus, the target bird always had a direct line of sight on us regardless of the overall habitat visibility. Our aim was to compare flight-initiation distances based on general habitat structure, rather than visibility from the bird's point of view. By doing so, the visibility was measured at chest height, which was not always at the same height as the bird. While we believe that our measure was associated with overall habitat structure, future studies may be able to use alternative techniques to get a better estimate of habitat visibility from the birds' perspective.

Furthermore, visibility may not necessarily be the most important factor in determining escape behaviour. Blumstein *et al*. (2004*a*) used eye size as an alternate measurement of visual acuity and found that this did not affect escape decisions. Less visibility may have made a bird more wary, but it did not carry over into escape decisions. Once the bird started to monitor an intruder, visibility *per se* may no longer be important and may not be involved in its subsequent escape decisions. Thus, it is interesting to note that there was no effect of visibility on detection as we measured it.

Prey may use other sensory modalities (i.e. acoustic, olfactory) to assess risk and these other modalities may be systematically influenced by some environmental factor. For instance, some species are more wary or less active when it is windy (Blumstein and Daniel 2003). This could result from an increased attentional cost (Dukas and Kamil 2000) because of movement in the surrounding vegetation, or it could result from an inability to hear approaching predators. Noise has been reported to modify behaviour in birds (Ward *et al*. 1999), mammals (Rabin *et al*. 2003) and amphibians (Sun and Narins 2005). While we did not study rosellas on excessively windy days, habitat-specific acoustic properties (e.g. Marten and Marler 1977), rather than visibility *per se*, may account for variation in foraging responses. It remains to be seen whether the acoustics of a specific habitat influence wariness while foraging and flight decisions. At this point, we conclude that visibility affects foraging behaviour but not escape responses in rosellas.

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