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Evaluating temporal and spatial margins of safety in galahs

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When approached by a potential predator, individuals must decide when to flee. Individuals could assess risk by monitoring their distance from an approaching threat or by monitoring the expected time that the predator would take to reach them. Theory predicts, and empirical studies support the hypothesis, that some species may maintain a temporal margin of safety and therefore monitor the expected time a predator would take to reach them. We systematically walked towards galahs, *Cacatua roseicapilla*, an Australian parrot, and varied our approach speed. If galahs maintain a temporal margin of safety, we expected them to flush at a greater distance in response to the fast approach. We found, however, no support for the temporal margin of safety hypothesis. Rather, we found evidence that galahs are sensitive to distance in a novel way: after being alerted, they flushed when humans approached to within 44% of the alert distance. Our result differs from traditional models of spatial margins of safety because it suggests that animals will take flight after being approached to within about half the alert distance. By doing so, individuals maintain a dynamic spatial margin of safety and may reduce costs associated with ongoing monitoring of predation risk.

When animals detect a predator, they may evaluate many factors to estimate the immediate risk of predation. In turn, the level of risk can influence the decision of when the animal should flee (Ydenberg & Dill 1986; Lima & Dill 1990). Flush distance (Holmes et al. 1993), the distance between the predator and prey when the prey begins to escape, is a commonly used measure of an individual's assessment of risk (e.g. Blumstein 2003) because it has been shown to vary as a function of risk. For example, Bonenfant & Kramer (1996) found that flush distance increased with distance to cover in woodchucks, *Marmota monax*, Cooper (2003) reported that the desert iguana, *Dipsosaurus dorsalis*, varied flush distance with directness of predator approach, and Diego-Rasilla (2003) found a positive correlation between flush distance and predation pressure in the wall lizard, *Podarcis muralis*. Although these studies show that flush distance is sensitive to variation in risk, they do not shed light on what mechanism animals use to assess risk. Identifying mechanisms of risk assessment is interesting because each mechanism may be subjected to unique constraints and trade-offs.

Broadly, an individual could assess risk by monitoring the time remaining before an impending attack or by monitoring the distance separating itself from the potential attacker. Both of these tactics require some knowledge of predator hunting behaviour. Some species are sensitive to the velocity of an approaching predator. Walther (1969) found that gazelles, *Gazella thomsoni*, have a longer flush distance in response to a fast predator than to a slow predator. Similarly, broad-headed skinks, *Eumeces laticeps*, desert iguanas and Bonaire whiptail lizards, *Cnemidophorus murinus*, have longer flush distances when approached at a fast speed than at a slow speed (Cooper 1997, 2003; Cooper et al. 2003). The findings that animals flush at greater distances when approached quickly suggest that animals assess risk temporally, because, for a given distance, a faster-approaching predator would reach them sooner than a slower-approaching predator. The evidence may also suggest that animals maintain a temporal margin of safety if the expected time to reach the individual is constant across speed treatments.

Dill (1990) investigated the temporal margin of safety concept directly in an experiment where the speed of a looming object was constant throughout the trials, but the subjects could control their escape velocity. He found that African cichlid fish (*Melanochromis chipokae*) did not vary escape velocity with respect to distance to cover, but they did flush at a greater distance the further away they were from cover. In support of his temporal margin of safety hypothesis, subjects appeared to choose a flush distance and escape velocity combination that allowed

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them to reach cover in a constant period of time. Bonenfant & Kramer (1996) investigated both temporal and spatial margins of safety in woodchucks by measuring the time and distance interval between the predator (an approaching human) and the woodchuck from the moment that the subject began to escape to the moment that the subject reached its burrow. Their results suggested that woodchucks maintained a spatial margin of safety.

Our study is unique in that we evaluated two possible mechanisms for assessing predation risk, and that we explicitly acknowledge that predators do not begin approaching prey at a fixed distance. We focused on the galah, *Cacatua roseicapilla*, an Australian parrot, to determine whether galahs assess risk by monitoring the distance between themselves and a predator or by monitoring the expected time a predator would take to reach them. We formally tested unique hypotheses about both temporal and spatial margins of safety to determine whether flush distance or time was constant across speed treatments for a given starting distance. In addition, we used those results to determine the assessment rule that was followed by galahs where both predator approach speed and predator starting distance varied.

METHODS

Location and Subjects

We studied galahs between 24 October and 5 November 2003 in and around Booderee National Park, Jervis Bay, Australia. The habitat consisted of open grassy areas and eucalypt forests. Galahs typically foraged on the ground, thus eliminating a possible confound that could influence predation hazard assessment (Blumstein et al. 2004). At these sites, galahs encountered people regularly and most appeared relatively habituated to humans. Although humans did not obviously harass galahs in and around Booderee National Park, Aboriginal Australians traditionally ate galahs (www.e-commkitchen.com/recipes/cuisineofworld/australian.htm). At our study site, galahs lived with the risk of predation by feral cats, *Felis catus*, red foxes, *Vulpes vulpes*, domestic dogs, *Canis familiaris*, and raptors (e.g. wedge-tailed eagles, *Aquila audax*).

Experimental Procedures

Our study sites were chosen based on relative galah abundance. We walked slowly in suitable habitat until a galah was spotted, whereupon we began the experimental approach. Galahs were typically found in groups of three (median = 3; range 1–9); three subjects were alone, and two were in a group of nine. For galahs in groups, we focused our approach on one subject. We looked and walked directly towards a focal subject at one of two different speeds: 1 m/s (hereafter, 'slow' approaches), and 2 m/s (hereafter, 'fast' approaches). We alternated our approach treatments between experimental trials. We dropped markers at the following three locations: (1) where we began our experimental flush, (2) where we were when the bird first looked up in response to our approach (which in some cases was equal to the distance when we began walking directly towards the bird), and (3) where we were when the bird flushed. Galahs' eyes are on the side of the head and thus they probably have a wide visual field (Fernández-Juricic et al. 2004). By scoring when a galah raised its head and oriented towards us, we quantified the location/time when a subject elected to cease its previous activity and orient towards us. We then walked to the bird's location at the start of the experimental approach, where we measured, in paces, the flush distance, alert distance and starting distance. Paces were converted to metres for analysis (all data collectors had similar paces). We timed our approaches with a stopwatch, and found that actual mean ± SD speeds in our final data set were 1.1 ± 0.13 m/s ($N = 20$) for slow approaches and 2.0 ± 0.14 m/s ($N = 30$) for fast approaches. We computed flush time (the time between the focal subject and the approaching person when the subject moved away) using the accurately calculated speeds.

Predictions

If galahs maintain a temporal margin of safety, we predicted that flush distance would vary between the two levels of predation risk. Specifically, we predicted that subjects would flush further when approached by a quickly moving person. The distance that an individual flushes in response to an approaching person is the result of a complex assessment process and is influenced by the distance at which the person begins walking towards them (Blumstein 2003). However, this 'starting distance' is correlated with the distance at which an animal initially responds to an approaching person (i.e. the alert distance), and alert distance itself is positively associated with flush distance in many species (e.g. Blumstein et al. 2004). Therefore, to properly study the effect of approach speed on flush distance, we focused on the interaction between approach speed and alert distance. We predicted that, if galahs maintain a temporal margin of safety, there must be a significant interaction between predator approach speed and alert distance on flush distance. If so, then we could conclude that approach speed influenced the expected interaction between alert and flush distance.

If galahs maintain a spatial margin of safety, we predicted that flush time would vary between the two levels of predation risk and that there would be no difference in flush distances. Again, we evaluated this hypothesis by examining the effect of the approach speed treatment on the expected relationship between alert distance and flush time. The fast speed was double the slow speed, so if risk increased linearly with decreased distance to the predator, we might also expect flush time for the fast approach to be half that of the slow approach.

Statistical Methods

Our final data set consisted of 30 fast and 20 slow flushes (we excluded some flushes for which we were unsure of the point at which birds first looked up).

Subjects were not marked, so we cannot guarantee that these 50 flushes came from different subjects. However, our impression was that there were several hundred galahs in the area, because galahs are very vocal and conspicuous when they roost, and people working in different locations simultaneously saw different groups of roosting galahs. A modest degree of pseudoreplication has been shown to not influence the results of studies like this (Runyan & Blumstein 2004). Our starting distances ranged from 11.4 to 42.6 m and were correlated with alert distances (Pearson correlation: $r_{48} = 0.622$, $P < 0.001$).

For each dependent variable (flush distance, flush time) we fitted a linear model with alert distance and the interaction of approach speed and alert distance as the independent variables. We forced these models through the origin (i.e. we eliminated the intercept) because a galah that first became alerted to an approaching person at 0 m could only flush at 0 m. Removing intercepts from general linear models, however, has ramifications for interpreting both main effects and interactions. We eliminated the main effect of approach speed from this model because when there is no intercept, the hypothesis being tested with a categorical factor is whether or not the intercept for each categorical factor is significantly different from 0 (this is an artefact of dummy coding algorithms in GLM routines). If the interaction was significant, we could interpret this as meaning that approach speed was responsible for the divergence. Linear models were fitted with SPSS 11.0 for the Macintosh (SPSS, Chicago, Illinois, U.S.A.). We interpret P values less than 0.05 as significant, and report partial η^2 as a measure of effect size.

RESULTS

We found no significant interaction between alert distance and predator approach speed on flush distance for the galahs ($P = 0.381$, partial $\eta^2 = 0.017$; Fig. 1). When we fitted a model without approach speed in it, we found that the slope of the relationship between flush distance and alert distance was 0.442 (95% confidence interval, CI = 0.388–0.496). We found a significant interaction between alert distance and predator approach speed on flush time for the galahs ($P = 0.028$, partial $\eta^2 = 0.101$; Fig. 2) where a fast approach resulted in a shorter flush time than did a slow approach. There was no main effect of flush time between speed treatments ($P = 0.436$), but the nonsignificant coefficient estimate for slow approaches (0.780) was about half that of fast approaches (1.468). Flush distance was also not affected by our treatment of speed ($P = 0.413$, partial $\eta^2 = 0.038$), yet it was positively correlated with alert distance (Pearson correlation: $r_{48} = 0.557$, $P < 0.001$). Thus, individual galahs maintained a set distance between themselves and the simulated predator for both levels of speed, but this distance increased with increasing alert distance. Specifically, galahs initiated flight when a human had approached to about half the alert distance.

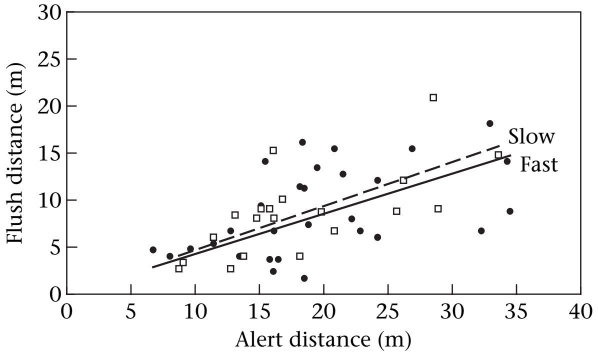

Figure 1. Effect of slow approach (□) or fast approach (●) on the relation between alert distance and flush distance in galahs.

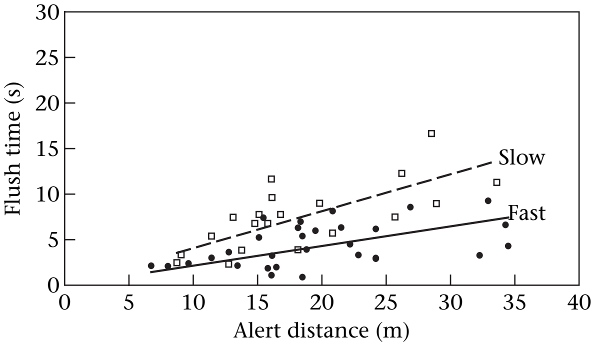

Figure 2. Effect of slow approach (□) or fast approach (●) on the relation between alert distance and flush time in galahs.

DISCUSSION

By not flushing immediately upon detecting a predator, animals may be able to assess the true risk of predation. Animals that are approached by a predator can assess risk of capture by estimating the time a predator would take to reach them, or by simply moving away when a predator comes closer than some fixed or variable threshold distance. We found that galah flight behaviour was flexible; both flush distance and flush time were positively correlated with alert distance. Despite this flexibility, galahs appeared to monitor aspects of distance, not time. Our evidence for this was that for a given alert distance, predator approach speed had no effect on galah flush distance. Thus, galahs did not maintain a temporal margin of safety, nor did they maintain a typical spatial margin of safety, which would be the case if they all flushed at a fixed distance. Rather, once alerted, galahs tolerated approach to about half the alert distance. Specifically, for all of our data, we found that the slope of the relationship between flush distance and alert distance was 0.44. This result suggests that galahs systematically assess risk for a given approach ratio of flush:alert.

This novel and initially unexpected finding is consistent with another recent discovery, that birds that are first approached at a relatively long distance also flush at a relatively long distance (Blumstein 2003). Flight initiation distance and alert distance are typically highly correlated (Blumstein et al. 2005), and optimal escape theory

(Ydenberg & Dill 1986) emphasizes that the relative costs and benefits of flight are expected to change dynamically. Thus, our results with galahs illustrate the dynamics of risk assessment. Rather than having a fixed escape distance, animals may be expected to modify it based on the relative costs to ongoing assessment. Thus, our results are consistent with the hypothesis that galahs maintain a dynamic spatial margin of safety. An alternative explanation for our result is that it takes time to assess the true risk of predation, and that galahs used a proportional distance rule when making this assessment.

Many species have the cognitive ability to assess time in a variety of contexts (Paule et al. 1999; Bateson 2003). However, maintaining a temporal margin of safety instead of some form of a spatial margin of safety may be more subject to error. To estimate the time a predator would take to reach them, individuals must estimate the predator's speed and assume that the speed and approach will be constant. If predators do not behave predictably, adopting a fixed or flexible spatial margin of safety may be a conservative strategy (Bouskila & Blumstein 1992) that may ultimately reduce predation risk.

Although our study is unique in how we studied the mechanisms of risk assessment, other researchers have reported results consistent with the hypothesis that animals maintain some form of a spatial margin of safety. Damselfish (*Chromis cyanea*) approached by a model predator at variable speeds did not vary their flush distance (Hurley & Hartline 1974). Bonenfant & Kramer (1996) found that woodchuck flush distance was not affected by approach speed.

Thomson's gazelles, *Gazella thomsoni*, are reported to have relatively fixed flush distances to various threats, and this invariance might be a result of experience with the threats (Walther 1969). In a national park setting, where humans travel around only in vehicles, gazelles tolerated closer approaches from people in vehicles than from people on foot. In contrast, in a park that also allowed visitors to move around on foot, gazelles flushed at similar distances in response to people on foot and in cars. It is likely that galahs at our study site were relatively habituated to humans and thus did not allocate time to evaluating the exact degree of risk associated with an approaching human. Rather, by adopting a dynamic spatial margin of safety (i.e. by having a fixed approach ratio), and by being sensitive to the distance at which they became aware of an approaching threat, the galahs adopted a conservative strategy that reduced their costs of ongoing risk assessment (e.g. Blumstein 2003). More generally, in cases where ongoing assessment is costly, we might expect that animals will generally adopt the error-prone but relatively simple rule of maintaining some form of spatial margin of safety.

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