Ethology

# The Fixed Slope Rule: An Inter-Specific Study

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## Abstract

There are two broad mechanisms by which animals can assess risk when deciding whether to flee: temporally and spatially. Animals that employ temporal mechanisms use predator speed to gauge threat. In contrast, those that use spatial mechanisms use the distance to the predator as an indication of danger. Traditionally, this was viewed as a fixed distance. Recently, a new type of spatial mechanism was proposed that focused on animals initiating flight at a fixed ratio of the distance at which they first responded to the threat. Our study investigated the consistency of this slope among three species: the Eastern gray kangaroo (*Macropus giganteus*), the Australian wood duck (*Chenonetta jubata*), and the Australian magpie (*Gymnorhina tibicen*). We found that these species exhibited statistically indistinguishable slopes from each other and the 0.44 slope that was initially reported in another species. Our results further support the assumption that escape decisions are dynamic. Future studies should determine the ubiquity of this fixed ratio.

## Introduction

The traditional view of antipredator flight behavior was that it was a somewhat static process controlled by inherent behavioral constraints (Ydenberg & Dill 1986). Under this perspective, flight initiation occurred at a fixed distance from a predator, based on the detection ability of the threatened individual. The idea of a fixed flight initiation distance later became formally known as maintaining a 'margin of safety' from a predator, the function of which was to protect the animal by keeping a constant distance between predator and prey (Bonenfant & Kramer 1996).

Ydenberg & Dill's (1986) work became the foundation of contemporary work on the decision to flee because it proposed an alternative model of prey response that was influenced by both costs and benefits of flight. Their model suggested that flight behavior was based on a dynamic rather than fixed assessment of predatory threat. It suggested that prey do not initiate flight at a fixed distance from a threatening predator, rather, they initiate flight based on an economic assessment of the costs of fleeing versus the costs of remaining in the presence of danger.

The idea of dynamic risk assessment proposes that flight initiation distance, the distance between an observer and a focal individual when it flees (hereafter FID), varies according to a variety of factors (reviewed by Stankowich & Blumstein 2005). Much empirical work has demonstrated that species may vary their FID based on both temporal and spatial assessments of predation risk. Recently, Cárdenas et al. (2005) proposed a novel type of spatial assessment, the fixed slope rule. Below we discuss temporal, spatial, and the fixed slope rule of risk assessment.

### Temporal Risk Assessment

Species that use a temporal mechanism to assess risk modify their FID based on the speed of predator approach (Bonenfant & Kramer 1996). Therefore, the faster a predator approaches prey, the greater the FID. While not experimentally confirmed, temporal factors of predation assessment were observed both in the lizard *Anolis lineatopus* (Rand 1964) and in various gazelle species (Estes & Goddard 1967; Walther 1969). Moreover, in a study of the desert iguana *Disosuarus dorsalis*, Cooper (2003) experimentally demonstrated that FID increased as the speed of predator approach increased. Similarly, Bonenfant & Kramer (1996) determined that woodchucks (*Marmota monax*) increased their temporal margin of safety as they moved farther away from their burrow. In this study, a temporal margin of safety was defined as the estimated time between the predator and the woodchuck at the instant the woodchuck reached its burrow. Interestingly, there are relatively few examples of temporal risk assessment; spatial risk assessment seems to be more commonly used by prey.

### Spatial Risk Assessment

Species that use a spatial mechanism to assess risk initiate flight based on the distance to the predator and/or from safety. This could work several ways. Many species are sensitive to the distance they are from cover when making escape decisions (Stankowich & Blumstein 2005). For instance, Dill's (1990) study of cichlid fish demonstrated that they maintain a constant spatial margin of safety from their cover by changing their FID but not their escape velocity. A variety of bird species initiated flight at a greater distance as initial starting distance increased (Blumstein 2003). Starting distance is the distance between the observer and the prey at the beginning of the trial. Although Blumstein (2003) demonstrated an interesting relationship between starting distance and FID, that study did not explore temporal factors that may have influenced responses to changes in the starting distance. Research on some species, however, eliminated the possibility of a temporal influence on escape behavior, confirming that some species assess risk using only spatial cues. For instance, a study of the escape responses in a damselfish, *Chromis cyanea*, found that reaction distance was independent of approach speed (Hurley & Hartline 1974).

### The Fixed Slope Rule

The idea of a fixed slope rule developed from a recent study of galahs (*Cacatua roseicapilla*), an Australian parrot, which tested temporal effects on the relationship between alert distance (AD) and FID (Cárdenas et al. 2005). AD is defined as the distance between the observer and the focal individual when the animal becomes aware of the approaching threat and visibly alters its behavior (Fernández-Juricic et al. 2005). Cárdenas et al. (2005) discovered a novel relationship between AD and FID in the galah population they tested. The slope of the linear regression between AD and FID was 0.442 (95% CI = 0.388–0.496). Thus, galahs consistently flushed at 44% of the AD regardless of approach speeds.

The slope of the regression analysis indicates how soon an animal flees after it becomes aware of an approaching predator. A steeper slope would indicate that animals initiated flight long after predator detection, whereas a slope closer to zero would indicate immediate flight. These findings suggest a new mechanism by which animals assess predation risk. The fixed slope allowed Cárdenas et al. (2005) to refute the hypothesis of temporal risk assessment because the slope of AD to FID remained constant regardless of varying approach speeds. Therefore, this slope rule illustrates a type of spatial rule where AD varies with FID. Our study further investigated this novel ratio between AD and FID by first determining whether spatial, and not temporal factors, were used by each species, and then by determining if each species exhibited an approximate 0.5 FID to AD ratio.

There is no a priori reason to expect a fixed ratio, and it is certainly meaningful to document these slopes because they could vary across species and be another way to describe a species variance (Blumstein 2006). Our study investigated this ratio in three Australian species: the Eastern gray kangaroo (*M. giganteus*), the Australian wood duck (*C. jubata*), and the Australian magpie (*G. tibicen*).

## Methods

Our study was conducted around Jervis Bay, Australian Capitol Territory, Australia (35°07′S, 15°44′E) between Oct. 19 and 30, 2005. Data on three species – Eastern gray kangaroos, magpies, and wood ducks – were primarily collected from the naval base golf course and the surrounding areas constituting H.M.A.S. Creswell, a small naval college. Additional magpie and wood duck data were collected from the Jervis Bay Naval Landing Strip as well as Green Patch and Iluka – two recreational sites in Booderee National Park, Jervis Bay. To reduce the likelihood of sampling the same subject multiple times, each area was sampled once, with the exception of Green Patch, which was sampled twice.

Our main site, consisting of the golf course and the surrounding Creswell areas, measured approximately 22 ha. Visibility was excellent and individuals of all species could be seen from afar. To ensure that we did not over-sample subjects, we censused kangaroos and wood ducks systematically, by walking through the open areas and noting all individuals. By doing so we obtained a minimum number of each species present. We concluded that we did not over-sample a species if this count was substantially larger than the number of individuals we tested. Magpies were censused by mapping territories because individuals were consistently found in the same regions of the sampling areas (Gibbons et al. 1998). We recorded the areas where magpies were encountered and then divided the area sampled into territories. Because we worked during magpie breeding season, we then multiplied the number of territories counted by two to obtain the minimum number of magpies.

We followed the Cárdenas et al. (2005) protocol and approached subjects quickly (2 m/s) and slowly (1 m/s). Different observers trained until their approach speeds were constant. Furthermore, each trial was timed to calculate the true velocity. An unpaired *t*-test was performed to confirm that the two speed treatments were significantly different.

We aimed to initiate our approaches from a wide range of starting distances. The trials were always performed on one focal individual. We only approached female kangaroos; however, both male and female magpies and wood ducks were tested. Because there was clear sexual dimorphism in wood ducks, we were able to determine if sex statistically influenced the relationship between AD and FID. All subjects foraged on the ground before they were experimentally approached. We defined an animal as alert when they clearly stopped foraging and picked up their head. While a single person collected data on approaches that began at distances less than 30 m, two people collected data on longer distance experimental approaches because it was difficult to detect the point at which the subject became alert to the observer and the point at which it initiated flight at longer distances. One member of the group would watch the subject through binoculars and inform the observer when the individual was alert and when it initiated flight. Markers were dropped at the starting point, the point at which the subject became alert to the observer, and the point at which the subject initiated flight. After the focal subject fled we continued to walk to where they were initially located. Starting distance, AD, and flight initiation distance were then calculated by measuring the distances between markers in calibrated paces and converting these paces to meters.

We fitted a general linear model in SPSS 10 (SPSS, Inc. 2000). We tested the effect of speed in influencing the relationship between AD and FID by modeling FID as a function of AD and the interaction between AD and speed. The models were forced through the origin because FID would logically be zero if AD were zero. Following Cárdenas et al. (2005) we did not include the main effect of speed. We did this because by removing the intercept, the main effect of speed only tested the hypothesis that the intercept was significantly different from zero. By contrast, the interaction directly tested the hypothesis that approach speed influenced the expected relationship between AD and FID.

In no case did speed explain significant variation in the relationship between AD and FID. Thus we regressed AD against FID and we obtained 95% confidence intervals for the beta values for each regression analysis. Overlap of these intervals would indicate the possibility that the beta values obtained for each species are statistically indistinguishable. Residuals for each calculation were plotted and visually inspected. All residuals were normally distributed.

Additional linear models were fitted to determine if other parameters explained variation in FID. To do so, we added the interaction between each parameter and AD to the basic model. For kangaroos, we tested if the number of conspecifics within 10 and 50 m affected FID (Blumstein & Daniel 2002). For wood ducks and magpies, we tested if the number of conspecifics within 10 m affected FID. For wood ducks, we also tested the relationship between AD and sex. Significance was inferred by a value of $p < 0.05$ and we report partial $\eta^2$-values to describe the effect size of a given parameter (Cohen 1988).

## Results

### Eastern Gray Kangaroo

Starting distances ranged from 23.1 to 215.3 m, and AD ranged from 16.4 to 142.3 m. In addition, the two speeds (fast: $2.0 \pm 0.16$ m/s, $N = 17$; slow: $1.0 \pm 0.12$ m/s, $N = 21$) at which we approached kangaroos were significantly different ($p < 0.001$). The effect of the interaction between speed and AD

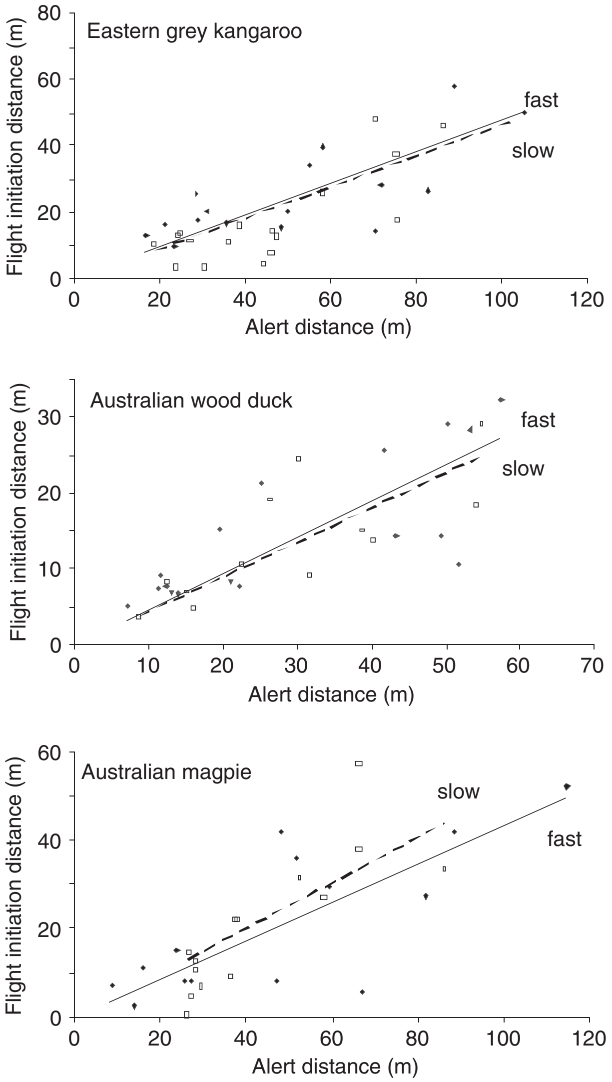

**Fig. 1:** Relationships between alert distance and flight initiation distance when approached quickly (solid diamond) and slowly (open square) for Eastern gray kangaroos, Australian wood ducks, and Australian magpies.

on the FID of kangaroos was not significant (Fig. 1; $p = 0.826$; partial $\eta^2 = 0.002$). AD alone, however, significantly affected FID ($p < 0.001$; partial $\eta^2 = 0.877$). We found that the FID of kangaroos was not significantly effected by the number at conspecifics within 10 m ($p = 0.736$; partial $\eta^2 = 0.004$) or 50 m ($p = 0.637$; partial $\eta^2 = 0.008$) of the focal subject. When we regressed AD against FID, we obtained a slope of 0.425 with a 95% confidence interval of 0.367–0.484. The maximum count of kangaroos was 153 individuals and 34 individuals were tested; subjects were unlikely to have been re-sampled.

### Australian Wood Duck

Starting distances ranged from 11.5 to 115.7 m, and AD ranged from 6.9 to 97.1 m. We only considered data points with ADs less than 70 m as those with ADs greater than 70 m appeared to reach an asymptote. An asymptotic function would suggest either that animals were unconcerned with threats above a certain distance, or that they could not detect the threatening stimuli (Blumstein 2003). In either case, it is not relevant to study the dynamics of risk assessment in this region. When plotted, the data collected above 70 m seemed to plateau with a slope close to zero. In addition, the two speeds (fast: $2.0 \pm 0.11$ m/s, $N = 18$; slow: $0.9 \pm 0.08$ m/s, $N = 15$) at which we approached kangaroos were significantly different ($p < 0.001$). The interaction between speed and AD on the FID of wood ducks was not significant (Fig. 1; $p = 0.771$; partial $\eta^2 = 0.003$). AD alone significantly affected FID ($p < 0.001$; partial $\eta^2 = 0.886$). We also found that the number of conspecifics within 10 m of our focal subjects did not significantly explain variation in the relationship between AD and FID ($p = 0.180$; partial $\eta^2 = 0.068$). When we included the interaction between the sex of the wood ducks and AD (sex × AD) to our model, we found it explained no significant variation in FID ($p = 0.164$; partial $\eta^2 = 0.073$). When we regressed AD against FID, we obtained a slope of 0.468 with a 95% confidence interval of 0.405–0.531. We counted 39 wood ducks at H.M.A.S. Creswell and tested 29 individuals; some subjects may have been inadvertently re-sampled.

### Australian Magpie

Starting distances ranged from 23.6 to 142.8 m, and AD ranged from 8.3 to 114.5 m. In addition, the two speeds (fast: $1.9 \pm 0.15$ m/s, $N = 16$; slow: $1.0 \pm 0.13$ m/s, $N = 14$) at which we approached magpies were significantly different ($p < 0.001$). The interaction between speed and AD on the FID of magpies was not significant (Fig. 1; $p = 0.291$; partial $\eta^2 = 0.043$). AD alone significantly affected FID ($p < 0.001$; partial $\eta^2 = 0.862$). We also found that the number of conspecifics within 10 m of our focal subjects did not significantly explain variation in the relationship between AD and FID ($p = 0.812$; partial $\eta^2 = 0.002$). When we regressed AD against FID, we obtained a slope of 0.466 with a 95% confidence interval of 0.390–0.541. Eleven magpie territories were found on the golf course, indicating at least 22 subjects. Twenty-eight magpies were sampled; subjects were inevitably re-sampled.

## Discussion

We found that Eastern gray kangaroos, wood ducks, and magpies used only spatial mechanisms for risk assessment. We ruled out temporal mechanisms because there was no significant interaction between approach speed and AD. Because the 95% confidence intervals for each species overlapped, we conclude that the regression slopes were statistically indistinguishable. These confidence intervals also overlapped with the 0.44 slope found in a recent study of galahs (Cárdenas et al. 2005). This indicates that this slope may be a general interspecific trait, and warrants future research with other species.

We found, however, that the slope for wood ducks was not maintained at distances greater than 70 m. This may indicate the existence of three zones of predator awareness in animals (Blumstein 2003). The first and closest zone to the animal is that in which the risk of remaining is too great and the animal must immediately flee. The second zone, directly beyond the first zone, is one in which the animal assesses the costs and the benefits of flight as described in Ydenberg & Dill (1986). The third zone is the farthest from the animal and is where the animal is not threatened by predator approach or cannot detect approach. We hypothesize that the third zone in wood ducks occurs beyond 70 m. We did not observe this third zone in magpies or kangaroos; their third zone must occur beyond the starting distances used in the study. In fact, when we emerged from cover, we often found that kangaroos were already aware of us. When this occurred, we delayed our approach until the kangaroos relaxed and resumed foraging.

Confidence in our results was tempered some extent because of some un-avoidable pseudoreplication. However, Runyan & Blumstein (2004) observed that a small amount of re-sampling has negligible effect on such FID analyses. Therefore, we do not believe that this greatly affected our results.

Our findings may have important implications for conservation and wildlife management, particularly for the creation and maintenance of nature preserves. Such protected areas are created to minimize the negative impacts of human activity on wildlife, such as a reduction in breeding success (Giese 1996) because of decreases in foraging (Lord et al. 1997; Blumstein et al. 2005) and increases in energy costs because of flight responses (Webb & Blumstein 2005).

Buffer zones are a common component of nature preserves and are created to reduce human access and associated negative consequences. Several methods are used to calculate buffer zones, but all take into account the FID of target individuals (Fernandez-Juricic et al. 2005). For example, Fox & Madsen (1997) suggested that buffer zones should encompass an area three times the FID of the least tolerant species. Fernández-Juricic et al. (2005) maintain that this method is fundamentally flawed because it failed to consider the distance at which species become alert to an approaching predator. AD is important to consider because vegetation or other obstructions could influence habitat visibility and this could change FID. But AD and FID themselves are somewhat static. The fact that there is a relationship between AD and FID suggests that buffer zones should not be based simply on AD. Therefore, wildlife managers may use the slope of the relationship between AD and FID to help create buffer zones to minimize the effects of human disturbance on animals.

While the four un-related species studied have statistically indistinguishable slopes, this does not necessarily mean that all species respond similarly. Flight initiation distance itself is influenced by a several life history and natural history traits (Blumstein 2006). Thus, our results call for a more comparative study of the relationship between AD and FID. Such studies should ideally first refute the hypothesis that a given species is using a temporal mechanism. With more broadly comparative results, we will be in a better position to design buffer zones for conservation as well as to better understand factors responsible for diverse antipredator behavior.

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