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Cover Page Footnote

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Flight Initiation Distance Differs between Populations of Western Fence Lizards (*Sceloporus occidentalis*) at a Rural and an Urban Site

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For a given animal, life consists of a series of decisions and compromises made in an effort to maximize fitness. These include decisions about how much time and energy to apportion to foraging, reproduction and associated social activities, and when to abandon these resources in the presence of a predator. The decision of when to flee is critical to the fitness of an individual (Cooper and Whiting 2007). According to escape theory, there is a balance between the cost of fleeing and the chance of being caught (Dill 1974); this tradeoff results in a decision as to how close a predator should be permitted to approach before initiating flight behavior (i.e., flight initiation distance; Ydenberg and Dill 1986, Cooper and Frederick 2007). Furthermore, there is a tradeoff between the antipredator behaviors of crypsis and flight; namely, when an animal initiates flight, it increases its likelihood of being detected by the predator (Martín et al. 2009).

Flight initiation distance (FID) is a trait that varies between populations and can be affected by factors including vegetation cover, type of predator, and predator density and efficiency (Blázquez et al. 1997, Diego-Rasilla 2003, Camp et al. 2012). Flight initiation distance has been studied in lizards extensively (e.g., Cooper and Whiting 2007, Martín et al. 2009, Cooper 2010, Cooper 2011). Generally, in populations exposed to higher predator densities, lizards are more wary and display longer FIDs (Diego-Rasilla 2003); that is to say, they initiate flight behavior while the predator is farther away, as compared to those in environments with lower predator densities.

In many animals, predation response is specialized (e.g., Walther 1969, Ghalambor and Martin 2000). The Western fence lizard (*Sceloporus occidentalis*) can distinguish between potential predators using visual cues about size and movement patterns (Fitch 1940, Fine 1999). This small, primarily insectivorous lizard is ubiquitous in open, sunny habitats west of the Rocky Mountains (Stebbins 2003). Common predators of this widespread species include snakes (e.g., racers, kingsnakes; Fitch 1940), mammals (e.g., foxes, raccoons, shrews; Nussbaum et al. 1983), and birds (e.g., kestrels, shrikes; Fitch 1940, Cooper and Whiting 2007). While encounters with humans may result in the occasional removal of an individual from a population (e.g., collection for the pet trade or incidental death), humans do not generally play the role of predator for Western fence lizards. Consequently, at sites with regular human activity these lizards should not view humans as dangerous predators and FID in response to humans should be reduced. Since flight for FID studies is usually initiated by a human researcher, it would be useful to determine if lizard FID responses differ between populations exposed to different human densities. This information would determine if it is necessary to choose study sites with similar human activity levels in order to remove unnecessary site bias from a study. We measured the flight initiation distances of lizards from two populations of Western fence lizards with different human exposure to determine if there was a difference in FID between the

two. Based on escape theory, we predicted that FID would vary with the population's exposure to human presence.

We conducted our study along fence lines at Snobird Lane in the San Luis National Wildlife Refuge, Merced Co., California (rural site), and at Taylor Road in Turlock, Stanislaus Co., California (urban site) during April-June, 2013. The rural site consisted of 763-m of barbed wire fence line along a dirt road separating an active almond orchard and the cattle-grazed grasslands of the wildlife refuge. This dirt road connects to a two-lane highway and serves as an access point to the refuge. Dense vegetation was available for cover around and between fence posts. The urban site consisted of 1150-m of concrete wall located along a sidewalk with regular foot traffic separating an urban residential area and an irrigation canal paralleling Taylor Road. Taylor Road is a busy two-lane street bordering farm land. We conducted our study on the foot path along the heavily vegetated side of the wall.

Each site was visited three times, and temperature, cloud cover, and wind speed were recorded. All observations were made in temperatures ranging between 25.6–35.2°C. On each sample day, we slowly walked the fence line searching for Western fence lizards. Once we observed a lizard, one observer walked slowly toward it until the lizard fled. If the lizard did not flee by the time the observer was directly in front of it, the observer left the path and directly approached the lizard until it fled. Flight initiation distance, the straight line distance between the researcher and the lizard's initial position, was measured using a laser rangefinder (Leica DISTO E7400x, Leica Geosystems, Heerbrugg, Switzerland). To avoid pseudoreplication, we only recorded FIDs of Western fence lizards encountered while walking in one direction along the fence line. In order to assess potential predation threats at each site, we also recorded all observations of predatory birds near enough to be reliably identified. Because the FID data were not normally distributed and transformations did not correct this problem, we used a nonparametric Mann-Whitney U test (SPSS 21, IBM Corporation, Armonk, USA) to test for a difference in FID between the two study sites. We used a Student's t-test (SPSS 21, IBM Corporation, Armonk, USA) to determine whether the abundance of predatory birds differed between the two sites.

We measured FID for 29 lizards at the rural site and for 65 lizards at the urban site. The Western fence lizards observed included males and females ranging from subadult to adult at each study site. At the rural site the average FID was 9.69-m (range: 1.35–30.45-m) At the urban site the average FID was 3.57-m (range: 1.02–8.38-m; Figure 1). Western fence lizards at the rural site initiated flight at a significantly longer distance than those at the urban site ($z = -3.44$, $df = 102$, $p < 0.001$). Predatory birds were significantly more abundant at the rural site ($t = 1.443$, $df = 5$, $p = 0.027$), where an average of 5.2 predatory birds were observed per hour (range: 1.30–12.3 birds/hr). At the urban site, there was an average of 0.5 predatory birds observed per hour (range: 0–0.8 birds/hr).

Many factors can influence FID, and lizards in areas with substantially different environments would be expected to exhibit different levels of wariness (e.g., Cooper and Whiting 2007, Camp et al. 2012). In this study, FID was found to differ significantly between study sites, with lizards at the rural site fleeing sooner than those encountered at the urban site. This difference in behavior can be attributed to each population's environment which differed in exposure to people and in predatory bird abundance.

Lizards have the ability to distinguish between potential predators (Fitch 1940, Fine 1999) and animals are known to alter their antipredator responses based on previous experience with that predator (Deecke et al. 2002). Flight initiation distance varied with

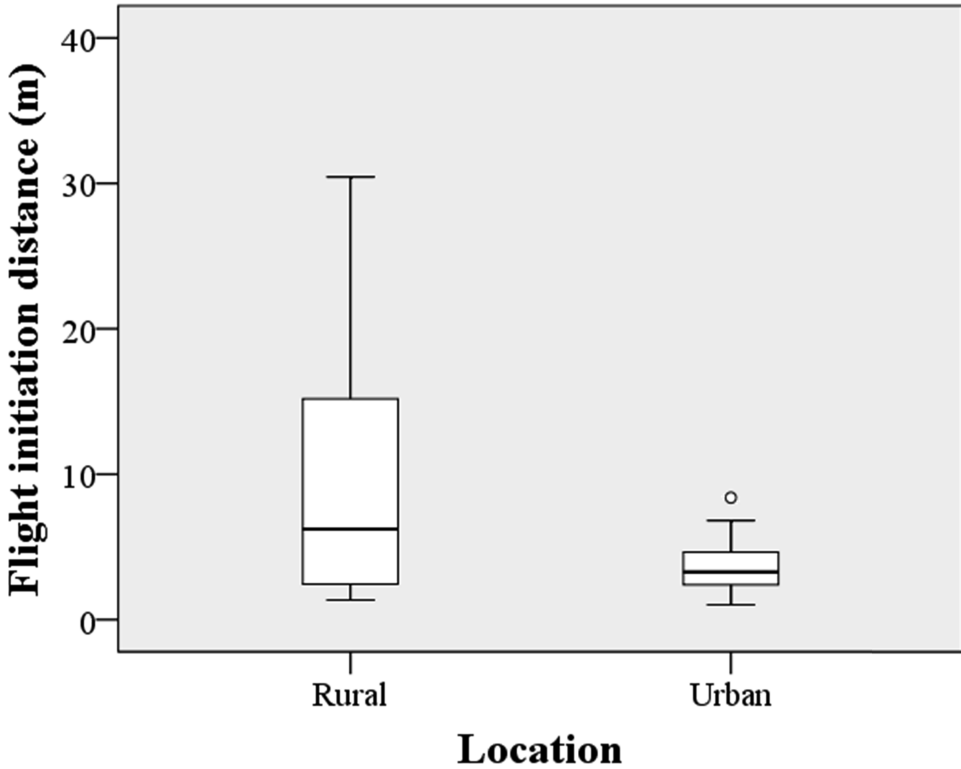


Fig. 1. Western fence lizards (*Sceloporus occidentalis*) at a rural site exhibited significantly higher flight initiation distances ($z=-3.44$, $df=102$, $p<0.001$) compared to urban lizards, and rural site lizards exhibited a wider range of responses. The open dot represents an outlier with a high FID at the urban site.

levels of human use, with lizards at the rural site exhibiting longer FIDs than those at the urban site. At the urban site, there is nearly constant foot traffic along the sidewalk where the lizards were surveyed. These humans generally ignore the lizards and pose little to no threat to the lizards' survival. Following the optimum escape theory, it is expected that lizards that do not view humans as high risk predators would allow humans to approach closer before fleeing than lizards in a naïve population; this behavior allows them to utilize their resources for longer. It follows that the population of lizards at the urban site would have a higher tolerance of humans, which is supported by their shorter FIDs (Figure 1). These results are consistent with studies on other taxa which demonstrate that squirrel (Engelhardt and Weladji 2011) and bird (McGiffin et al. 2013) tolerance of humans varies with level of exposure.

Alternatively, at the rural site, lizards rarely encounter people on foot and so have little individual experience on which to base their decision on when to flee to maximize fitness. With little human traffic, the population would not have been under selection for reduced wariness in response to humans, and without a human-specific antipredator response, the lizards at the rural site must rely on general antipredator responses. According to Dill (1974), prey species have evolved general antipredator responses to stimuli such as approaching objects and loud noises. These responses vary with the intensity of the stimuli following the same risk/economic scale used for recognized predators. Based on this theory, it is predicted that the naïve population would have longer FIDs than the

population with experience of the harmless human stimuli; the population would not have evolved a lack of wariness in the presence of humans. Our data are consistent with this prediction. Furthermore, the greater variance in FIDs at the rural site suggests variation in individual perception of the danger posed by an approaching human; this is also consistent with a population in which the individual experiences of lizards with recognized predators are applied to produce a response to a human model.

The sites also have differences in avian predator abundance which could contribute to the differences in flight initiation observed. Diego-Rasilla (2003) found that predator density affects flight initiation distance in lizards such that lizards under higher predation pressure had greater FID. Our data support this finding, with the more predator-dense rural site having lizards with, on average, longer FIDs. However, this interpretation is tenuous in that only avian predators were recorded in this study. It is likely that other predators were present but not recorded in both the rural and urban sites (e.g., domesticated cats, raccoons, foxes, coyotes).

Flight initiation distances have been found to vary with other environmental factors such as percent vegetation cover (Cooper 2011, Cooper and Whiting 2007). Additional studies would be beneficial to tease out other variables that affect flight initiation distances of the Western fence lizards at these locations. It would be favorable to use several study sites across an urban-rural gradient. Observing lizards in a highly visited rural area, such as a national park, would help in determining which factors contribute most to FID. In addition, it would be useful to determine if there are differences in FID by sex and age. Since Western fence lizards are known to be territorial (Sheldahl and Martins 2000), FID may differ between those who defend their territory or their mates and those who do not. This study is significant in that it demonstrates that FID does differ between the rural and urban sites. Researchers interested in antipredator behavior should select study sites that lack regular human activity or choose methodologies that use a nonhuman model predator in order to collect meaningful data on lizard response.

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