The Ecology of Anti-predation of the Long-nosed Leopard Lizard, *Gambelia wislizenii*, a Mesocarnivore in Desert Scrub

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Female *Gambelia wislizenii* with a large meal, an adult *Aspidoscelis tigris*.

This one lizard prey item probably replaced much of the mass the female *G. wislizenii* expended during recent reproduction.

One *A. tigris* obviously is calorically worth many grasshoppers.

***Artemisia tridentata* (above) has less near-ground protective cover than *Sarcobatus vermiculatus* for refuging lizards.**

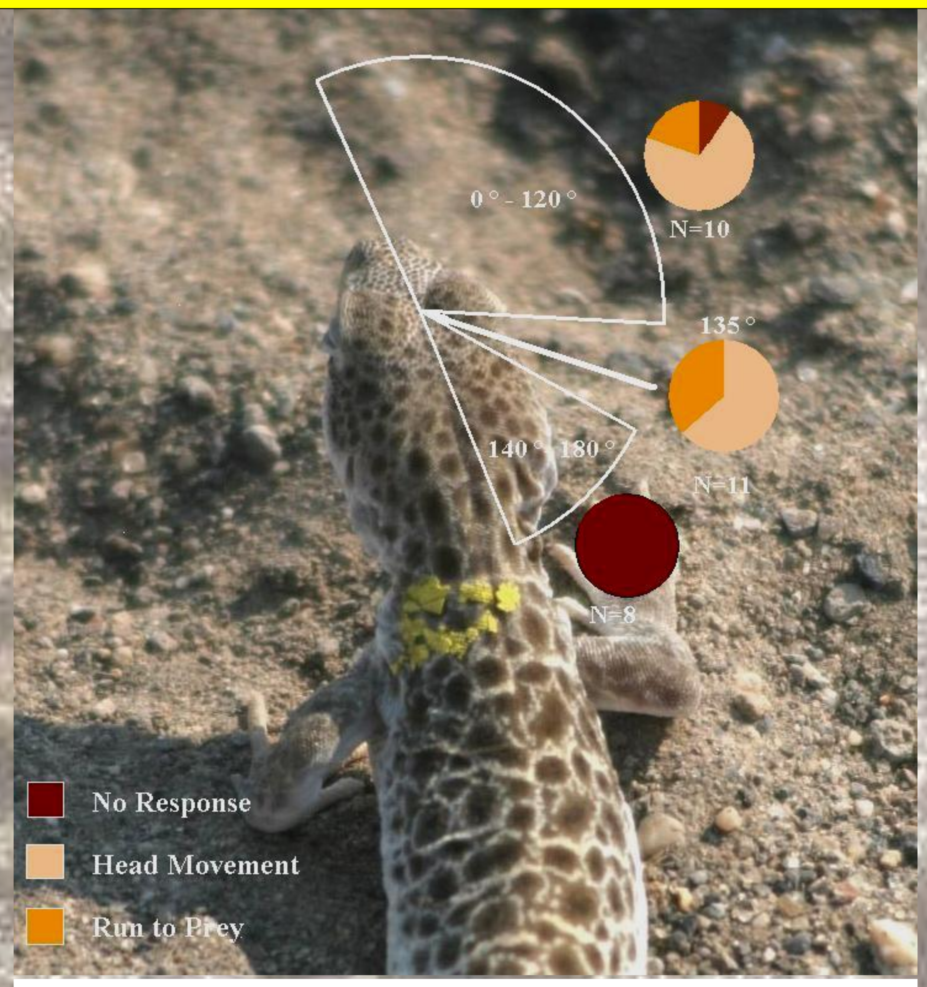


Figure 13. Test of field of view in *Gambelia wislizenii*: behavioral responses of *G. wislizenii* to the glint of nuts mimicking the flicker of insect wings. The nuts were held approximately two meters above ground and less than eight meters from the lizard. N = 16 lizards, 29 total trials.

***Sarcobatus vermiculatus* has dense and spiny branches near ground and serves as effective cover for refuging lizards.**

View from the west edge of the study site, looking west, upslope, toward Alvord peak; note greasewood, the lime-green shrub, within a veritable forest of the pale-green sage.

Introduction

One of the primary research goals in the field of ecology is understanding the distribution and abundance of organisms. Deserts are particularly useful for investigating the distribution and abundance of terrestrial organisms because 1) desert ecosystems are relatively simple, 2) the species diversity is low enough to develop an understanding of the organismal interactions, 3) the open aspect of the habitat—with perennial plants widely separated—permits observational-descriptive-comparative research on animals and plants to be of remarkably high quality, and 4) field experimental studies are relatively easy to perform.

In the northern reaches of the Great Basin Desert, in the Alvord Basin of southeastern Oregon are three abundant species of lizards that are easy to observe and capture: the long-nosed leopard lizard *Gambelia wislizenii,* the western whiptail lizard *Aspidoscelis tigris*, and the desert horned lizard *Phrynosoma platyrhinos*. The locale chosen for studying lizard behavior is an ecotone between the upslope habitat dominated by the Basin Big Sage (*Artemisia tridentata*) and the basin-bottom dominated by Greasewood (*Sarcobatus vermiculatus*) .

Gambelia wislizenii is a meso-carnivore, feeding primarily on 1) large, day-active arthropods such as grasshoppers and robber flies, and 2) lizards, even feeding on subadult *G. wislizenii*. *Gambelia wislizenii* is extremely tolerant of the presence of humans, and is easily observed under natural conditions. Hence, it is an excellent focal species for studying organismal interactions. *Gambelia wislizenii* is an ambush predator and detects prey largely by vision, and primarily by the movement of its prey. Predators are presumably detected by vision as well.

As a mesocarnivore, *G. wislizenii* is a potential prey for raptors and snakes. The competing endeavors of *G. wislizenii* to seek prey and to avoid becoming prey provides some intriguing research opportunities. Knowing the limits to the leopard lizard's ability to detect prey and predators would be necessary knowledge in the endeavor to understand the adaptedness of the lizard's movements and ambush positions that it uses throughout its daily activity period. And establishing the visual field used by *G. wislizenii* would be particularly useful in our efforts to understand the functional relationship of this mesocarnivore to its prey and predators.

Although the frequency of encounters of *G. wislizenii* with predators is apparently extremely low, it was expected that *G. wislizenii* would readily respond to an apparent pursuit by either an ersatz surface predator (e.g., human) or an aerial predator. We expected the leopard lizard to display distinctly different behaviors in varying microhabitats, such as when in the open compared to when under the cover of a shrub.

Because *G. wislizenii* has eyes oriented slightly forward, we expected we would be able to determine the limits to their visual field, posteriorly, and thus provide evidence that lizards would be more vulnerable to attacks by predators from above-and-behind. And because most open areas average about 10m in this habitat, we expected that these lizards would not respond strongly to faux-prey at distances beyond this 10m perimeter. Hence, in addition to examining evasion responses of leopard lizards under natural field conditions, we planned three sets of tests: 1) simulated attacks of aerial predators, 2) simulated glint of wings of a large insect in flight, and 3) the nearby landing of a live grasshopper onto the sand.

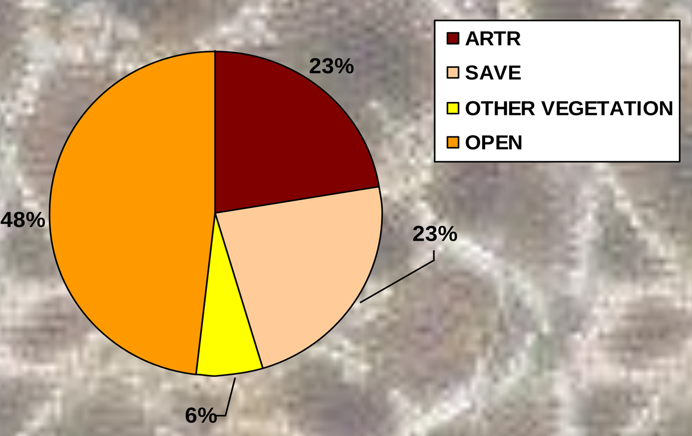


Figure 1. Distribution of microhabitats used among *Gambelia wislizenii* (N = 35 lizards) just prior to behavioral response experiments. ARTR is the basin big sage, *Artemisia tridentata*, it is the most common shrub, but foliage tends to be less densely protective. SAVE is the greasewood, *Sarcobatus vermiculatus*, it has dense protective cover.

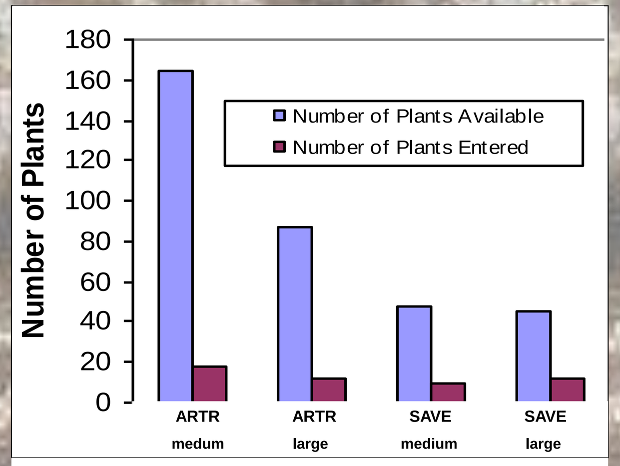


Figure 2. Distribution of plants near the evading (human–pursued) leopard lizards that were available v. plants used for a refugium (N = 60 lizards).

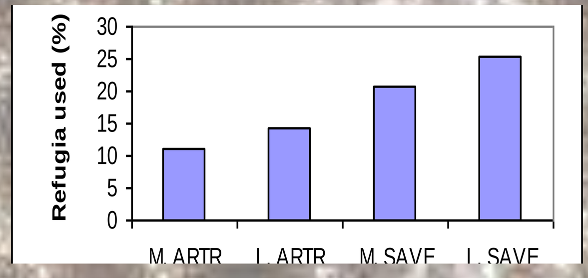


Figure 3. Distribution of refugia used by evading leopard lizards.

Figure 4. Evading lizards did not tend to enter the nearest perennial

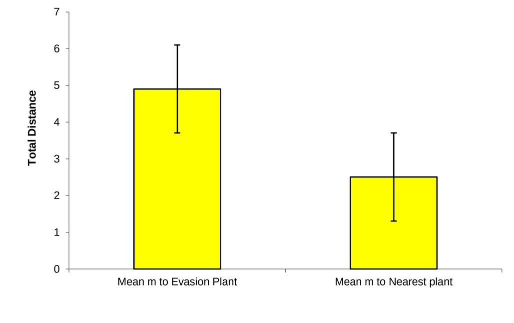


Figure 5. Perennial plants entered by evading lizards tended to be larger than the nearest perennial.

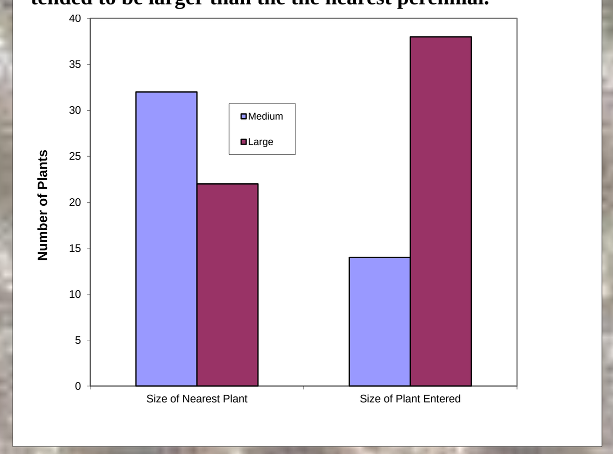
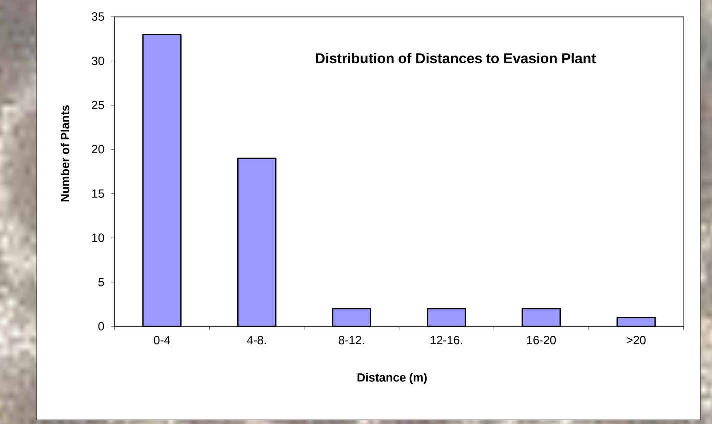


Figure 6. Most refuge plants chosen by *Gambelia wislizenii* were generally within 5m.



Results

Initial conditions and spatiotemporal patterns of evasion in response to a surface-running "predator": Figures 1 – 9, and Table 1.

Most lizards were in the open when searching for prey during mid-morning, when activity did not have to be restricted to sunlit locations (as in cool conditions) or in shade (in hot conditions), as shown in Figure 1. Evading *Gambelia wislizenii* tended to use larger more densely vegetated shrubs for cover, that is, the larger *Sarcobatus vermiculatus.* Leopard lizards also commonly ran around the shrub and out of sight of the human pursuer. We rarely witnessed bipedal runs, presumably because distances to cover were short (and perhaps we were slow)and lizards were quickly circumnavigating the perennials.

Approach by aerial predator: Figures 10 & 11

When approached by a model of an aerial predator, most lizards responded by moving at least one body length in an attempt to evade the "predator" . In all three types of predator approach, however, some lizards appeared to show no movement in response. Leopard lizards in the open usually sought refuge under shrubs when approached by our aerial "predator," and they moved much further than lizards that were already under cover of shrubs (values were significantly different, at 0.05 level, with a t-test).

The glint of dangling hex nuts as simulated wing flash of insects: Figures 12 & 13.

Gambelia wislizenii responded more predictably and vigorously to the shiny, jiggling hex nuts when the nuts were displayed within 10m and within 5m all lizards noticed the nuts (Figure 5). And no lizard when presented with the nuts at horizontal angle (0° was directly anterior, 180° was directly posterior) greater than 140 degrees displayed any response (Figure 6). Nuts were presented at $\leq$135° resulted in head turns and pursuits. Note that all eight individuals with no reaction and that were tested first at 12 m or greater responded in the second, nearer test. The other four first tested at 12m or greater responded the first time, but with head movement only.

Table 1 *Field Pursuit Measures*	Evasion Distance (m)	Evasion Velocity (m/sec)
Mean	7.4	2.15
Range	0.74 - 44	1 - 5.2
SD	9	1

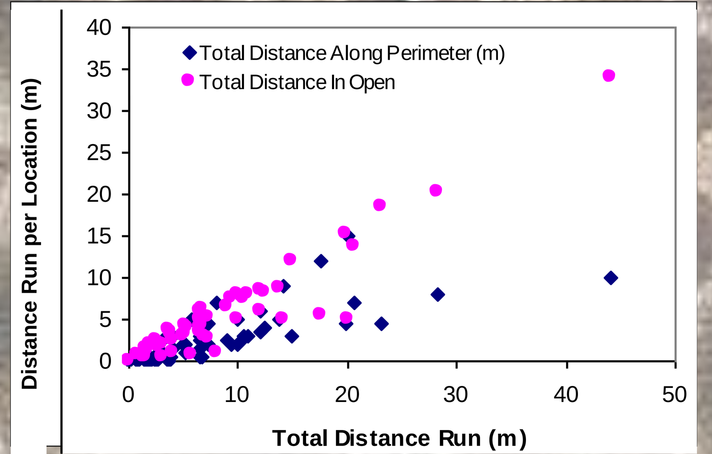


Figure 8. Distances run were a combination of quadrupedal and bipedal runs in the open and quadrupedal runs along plant perimeters .

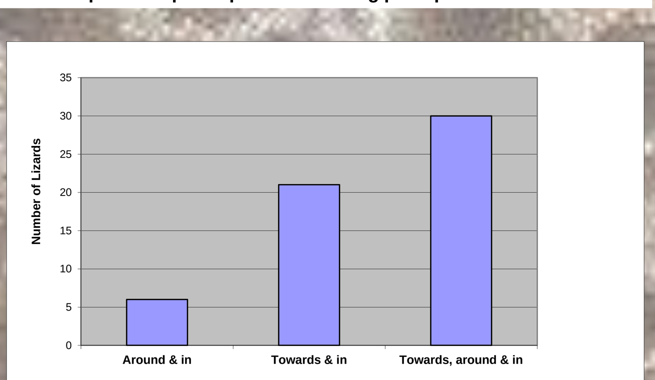


Figure 9. More evading leopard lizards ran along the perimeter of a perennial before entering than ran straight into the plant.

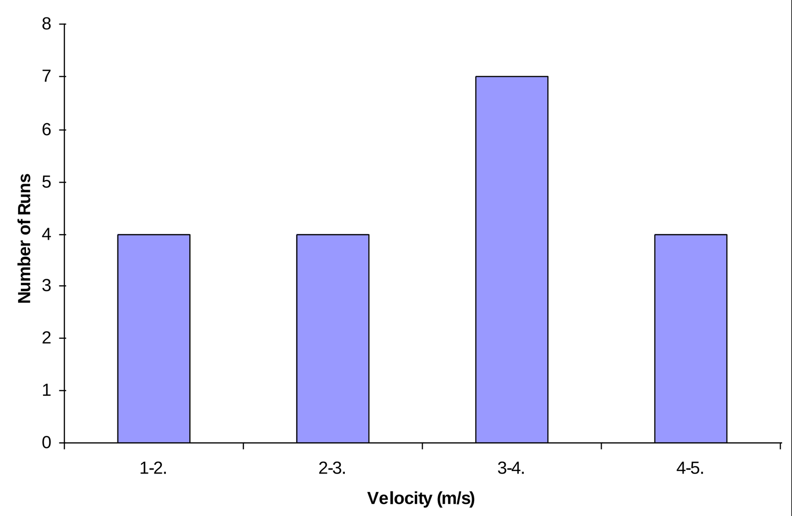


Figure 7. Velocities of 21 *Gambelia wislizenii* "chased" in a 20m field raceway on natural sand substratum. Data are best velocities among 3 trials.

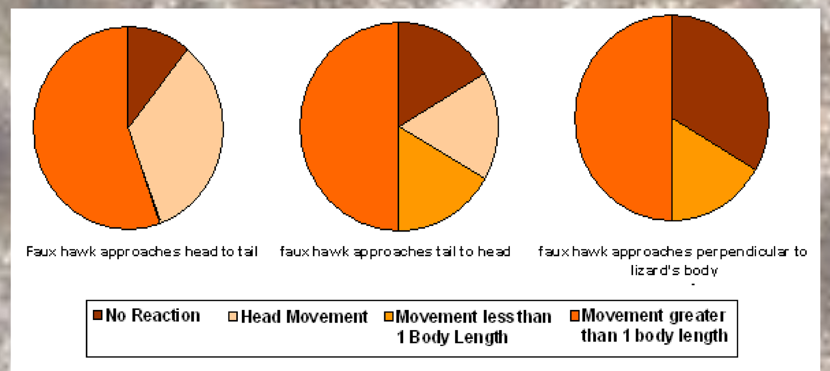


Figure 10. Comparisons of types of behavioral responses by *G. wislizenii* to an ersatz aerial predator (mock hawk) approaching from one of three directions. Most lizards were in the open when tested, but because among-microhabitat behavioral responses of lizards were not statistically different, the data on lizards in open and under canopies of shrubs were pooled. N = 35 lizards.

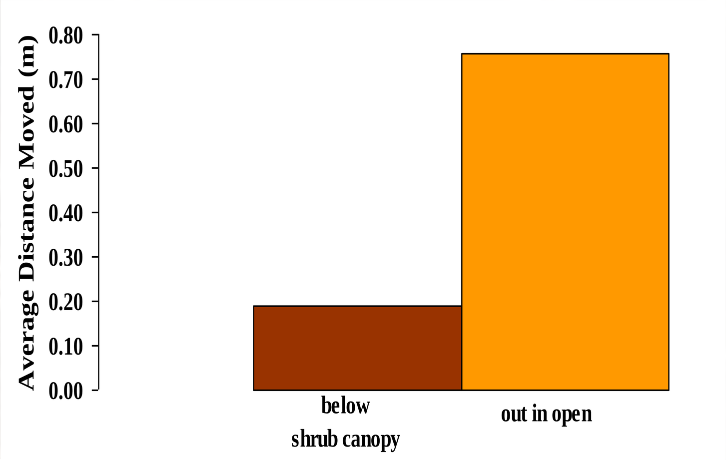


Figure 11. Comparisons of evasion run distances of *G. wislizenii* in response to mock aerial predators when lizards were in the open versus under shrub cover

Materials and Methods

Field Chases:

***Gambelia** wislizenii* were chased in the three main mesohabitats to observe their behaviors and evasive strategies, routes were marked by dropping flags, and the flagged routes were mapped utilizing some vegetation maps from previous years, and hand making a few small sections this year in the field.

Raceway Runs:

The raceway consisted of a 20 meter long track with natural sand substratum. The finish line was decorated with dead wood and common desert shrubs to look shady and green. Cameras above the racetrack recorded the runs, which were reviewed later to measure the velocities of the lizards running in the track. Lizard were set on the sand and ran without much provocation. Stopwatches were used to measure velocity of lizards over the entire run distance.

Trials with a faux hawk in an aerial, diving pursuit of the lizard on the ground:

The visual detection-and-response of *Gambelia wislizenii* to an aerial predator was tested with an ersatz bird-of-prey diving from atop a telescoping pole; the model predator moved along a monofilament zip line, first approaching, then passing over the lizard. A model of a space shuttle made of dense styrofoam was painted on the underside to resemble the underbelly of a red-tailed hawk.

The model predator was propelled along the zip-line by hand. The model was presented in an angled, diving pursuit, and was directed either parallel (tail-to-head or head-to-tail) or perpendicular (from the side) to the lizard. With a researcher holding the zip-line taught at either end, one tall researcher would stand about 5 m from the lizard and propel the model that had been raised about 2.5m above ground by a telescoping pole. The other researcher would catch the model at the down slope end approximately 0.25 m above ground and 1-2 m beyond the lizard. The zip-line was positioned so that the "mock hawk" would pass approximately 0.5m above the lizard.

Each lizard was tested only once to obtain one response to the aerial predator. We compared responses of lizards in two microhabitats: one test was on lizards in the open, and the other test was on lizards under shrub cover. A preliminary test was also conducted in which we oriented the hawk model so that the shadow of the model moved directly over the body of the lizard.

The glint of dangling hex nuts as simulated wing flash of insects, in an effort to determine visual field and visual response distances:

The response of *Gambelia wislizenii* to a simulated flying insect was tested with two shiny hex nuts loosely tied together and suspended by microfilament line from a 3 meter fishing pole. Once the nuts were in the open they were gently rotated in order to reflect the sunlight so that they would sparkle (they did not produce a tinkling sound), thus mimicking the shine off of insect wings while in flight. For each set of tests, the lizard behaviors was recorded on Hi-8 tape.

If the lizard displayed no response (that is, no head movement, or body movement, or running towards the "prey"), the nuts remained visually exposed for a maximum period of ten seconds and were then hidden and moved to another location so that similar tests from smaller horizontal angles or closer distances were performed. Once a response in the form of a head, body, or running response was displayed, the nuts were immediately covered and removed from the lizard's sight.

Lizards on which two tests were performed were allowed to resume normal behavior after the first test, before they were presented with the nuts a second time. In a situation where there appeared to be no response to the dangling hex nuts, such as when the nuts were presented at an extreme angle or very long distance, the initial test would be followed by the nuts being presented at a less extreme angle or shorter distance at which the lizards were more likely to respond. A maximum of two trials of one of the three types of tests for each individual lizard were used for data analyses.

Each lizard was tested for one of three detection-and-responses. The two primary tests were 1) horizontal angle relative to the lizard's head, to determine the ability of the lizard to detect prey at extremes of peripheral vision, and 2) distance, to determine how distance affects the lizard's ability to detect prey (longest distances) and the lizard's response to these simulated prey at near and intermediate distances. We also performed preliminary tests to try to determine useful, perhaps optimal heights for response, so that height of presentation above the ground was not a factor for test types 1 and 2.

Leopard lizards commonly threat-gape, when handled and they usually bite when given the opportunity.

Male *Gambelia wislizenii* demonstrating the extension ability of its jaws needed to subdue *A. tigris* which may reach a body size equivalent to that of *G. wislizenii.*

The most commonly seen species of grasshopper during grasshopper count, above, may also be the most common prey taken by *Gambelia wislizenii*.

Adult male leopard lizard, cryptic and in classic ambush predator behavior: motionless while visually scanning for approaching prey

Discussion

Gambelia wislizenii when pursued as they were in the midst of their daily field activity period, and presumably at field active body temperature, demonstrated relatively standard evasion behavior: running to a larger nearby perennial, particularly the species that provided greater cover. The tendency to run along the perimeter of a perennial, curving out of sight before entering was an intriguing and perhaps common antipredatory tactic for prey species. We have anecdotally witnessed rabbits and deer perform the same maneuvers.

Leopard lizards in the open responded to the approach of "aerial predators" by rapid evasive runs to shrub cover, whereas those under or very near shrub cover moved a relatively short distance. Although more trials are needed to achieve statistically significant patterns, we are confident in our view that when a *Gambelia wislizenii* is approached by an aerial predator in the open it is more likely to exhibit an immediate prostration, body rotation, and evasion run than a lizard that is less exposed. The evasion behaviors may also differ, based on the direction from which the predator approaches. When a predator approached from the side, in full view, the *G. wislizenii* tended to move perpendicular to the direction of the predator approach and a also moved bit towards the predator. When the predator flew in from behind, the lizard usually moved forward. Our preliminary tests show there is rich potential for cleverly designed experiments with ersatz aerial predators. We also suggest "snake models," given that two species of snakes on site are likely to eat *G. wislizenii* on occasion.

At distances $\leq$ 5m, some *Gambelia wislizenii* apparently recognized that the jiggling hex nuts were not a potential prey item, even though they all generally responded to the nuts, usually by head movement, some did not perform a running pursuit of the nuts. Distances of five to ten meters had the most variable responses among lizards. Roughly one-fifth of all *Gambelia wislizenii* tested did not respond at all, and although the others ran toward the nuts, only a three lunged & leaped toward them in a true capture attempt. At greater distances, 12-17 m, half of the lizards responded with head movement and half did not respond. Thus we infer that these distances either 1) may be near the end of *Gambelia wislizenii's* ability to resolve detailed images, or 2) lizards "decide" that these distances are be too far to chase prey. Objects cannot generally be seen at longer distances because the view is obscured by shrubs. Hence, distances greater than 10 meters generally may not be relevant. Moreover, running toward a prey that is flying above and behind several shrubs is presumably problematic.

Based on our experiments with dangling hex nuts to determine the field of view for *Gambelia wislizenii*, we infer that *G. wislizenii* have a horizontal visual field of 270°, that is, 135° to both right and left, with 0° centered in front. No response was elicited beyond 135°, whereas all lizards responded with either head or body movement at $\leq$135°. Note from Figure 6 shows that a running response occurred more often at 135°, the extreme in the field of view; perhaps at nearer distances and less obtuse angles the lizards recognized that the nuts were really not like prey. This analysis included presentation of nuts at distances $\leq$ 8m, so that if in the field of view, a response was certain to be elicited.

Future research will focus on more comprehensive tests of running ability in the field (e.g., up steep dune slopes, and across open expanses) and on antipredatory reactions of leopard lizards to snake models.

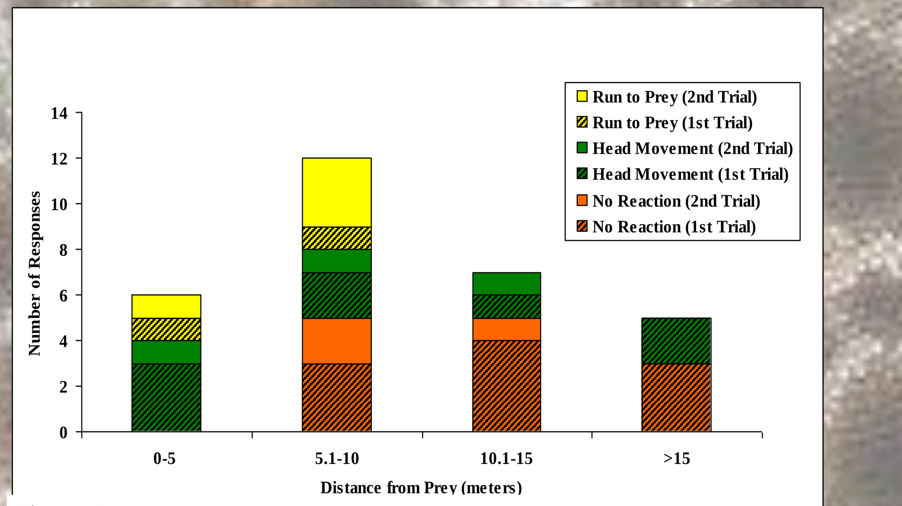


Figure 12. Investigating reaction distances: types of responses by *Gambelia wislizenii* to mock aerial insect prey, as related to initial distances from the "prey." Tests were performed within the horizontal visual field of about 270° (in front is 0°, so the field of view is in within an arc 135° to the right or left). Three visually obvious response categories were used. Some lizards were tested more than once, but the first test was always performed at a distance farther away from the lizard than the second test.