

Article

Escape Tactics Used by Blanched Lesser Earless Lizards (*Holbrookia maculata*)

Kaera L. Utsumi ¹, Daanya Siddiqui ², Janey B. Haddock ³, Makenna M. Orton ¹, Telma G. Laurentino ⁴, Maria A. Eifler ^{1,5} and Douglas A. Eifler ^{1,*}

¹ Errell Institute, Lawrence, KS 66047, USA; kaera.utsumi@gmail.com (K.L.U.); ortonmmakenna@gmail.com (M.M.O.); maria.eifler@gmail.com (M.A.E.)

² School of Public Health, University of Washington, Seattle, WA 98195, USA; dsiddi@uw.edu

³ Laboratory of Ecology and Behavior, Faculty of Science, Autonomous University of the State of Mexico, Toluca 50110, Mexico, Mexico; janey.haddock@gmail.com

⁴ CE3C—Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal; telma.laurentino@gmail.com

⁵ Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA

* Correspondence: deifler@erell.ngo; Tel.: +1-785-691-9161

Abstract

Successful escapes depend on many factors, including predator type and habitat characteristics. Examining escape usually entails directly pursuing an individual and then measuring flight initiation distance (FID), but the effect of prolonged pursuit has not been well studied. We examined escape sequences by blanched adult lesser earless lizards (*Holbrookia maculata*) in the Salt Basin Dunes (SBDs), testing the hypothesis that escape success and sequences would vary with sex and vegetation use. Their coloration is an adaptation to their sparsely vegetated white sand habitat. To evaluate escape behavior, we followed an individual directly until it disappeared (=successful escape), stopped moving, or 2 min elapsed. We recorded trial habitat (at the start and throughout), time to trial end, FID, length of moves, and total distance moved. FID varied with starting habitat—lizards beginning trials on exposed wood had the longest FID. The sexes differed in their move lengths: females made more short moves, while males made more long moves. The most important plant was sage (*Artemisia filifolia*), which was occupied at the start of 39% of trials, while 71% of trials ended in sage, and larger sage bushes supported longer escape sequences. Our study highlights the importance of vegetation for refuge and emphasizes the crucial role of the dune-plant landscape to lesser earless lizards.

Keywords: anti-predator; evasion; fleeing; flight behavior; risk assessment



Academic Editor: Michael Wink

Received: 22 December 2025

Revised: 24 January 2026

Accepted: 28 January 2026

Published: 30 January 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

1. Introduction

Predation is an important factor shaping the behavior of animals that can become prey [1]. Indeed, predation avoidance can be a major part of an animal's daily activities, with effective avoidance of predators helping to lengthen lifespan, while excessively conservative anti-predator strategies undermine other essential tasks [2]. Escape from predators should reflect both the cost of interrupting current activities to respond to predators and the relative risk of predation [3,4]. Costs that can factor into escape decisions include loss of access to food [5], loss of time and energy to engage in social activities [6,7], and loss of radiant heat when basking [8]. Predation risk can be affected by many factors, including speed, direction, and persistence of predator approach [9–11]; type of predator [12,13]; or habitat

characteristics [14]. Demographic characteristics such as sex and age also can play a role in the costs and perceived risks associated with escape behavior [7,15–17].

Flight initiation distance (FID) is a well-studied aspect of escape behavior. For many animals, deciding when to initiate escape is the primary decision that needs to be made, as escape maneuvers that follow can be simpler and more effective when escape is initiated quickly [7,18]. FIDs can be adjusted based on predator behavior, such as speed and directness of approach [11,19–23], as well as environmental factors, such as habitat composition and temperature [24–27]. The decision to escape is followed by additional decisions regarding how to complete the escape sequence, which can depend on situational factors [1,28]. When speed alone is insufficient (i.e., evader is physically unable to outrun pursuer), directional evasive maneuvers and refuges become important [1,29,30], with evaders continuing to assess the likelihood of capture as the escape sequence progresses. Prolonged escape sequences reflect an escalation in predation pressure [18] and can involve more complex maneuvers [31]. Many animals have more than one maneuver option, and discerning which to employ, under which conditions, is an important aspect of an escape strategy [16].

Many fleeing animals use refuges to escape predation; however, accessing a refuge does not guarantee safety, and decisions must be made about how to use and when to abandon the refuge. Refuges can be selected based on their characteristics relative to predation risk, such as refuge location [32–34], effectiveness at obscuring or protecting prey [9,24,35–37], and the probability of potential predators lurking in or around refuges [38,39]. Additionally, indices of predation risk, such as predator speed and persistence, can influence the use of and reemergence from a refuge [10].

We explored the escape decisions of lesser earless lizards, focusing on the traditional FID measurements, while also examining the behavior of individuals exposed to prolonged escape sequences resulting from persistent simulated predators. The common lesser earless lizard (*Holbrookia maculata*) is a sexually dimorphic, diurnal, insectivorous lizard that ranges across the Southwestern and Central United States and into Central Mexico, occupying habitats such as alkali flats, sand dunes, and grasslands [40–42]. Individuals exhibit distinct color morphs, ranging from dark brown to blanded white [41,43,44]. Two blanded populations have been described so far: one residing at White Sands National Park (WSNP), which has been relatively well studied [40,41,45,46], and a second of more recent interest [47,48] inhabiting the Salt Basin Dunes (SBDs) in Guadalupe Mountains National Park (GUMO).

The SBDs are composed of white gypsum sand, which contrasts with the darker substrate of the surrounding Chihuahuan Desert. The lesser earless lizards of the SBDs are blanded, possibly representing a genetically distinct lineage from adjacent populations, as well as from the similarly blanded lesser earless lizards at WSNP [47]. Compared to WSNP, the SBD habitat covers a smaller area and contains more heavily vegetated dunes. Both gypsum deserts have cryptobiotic-crust-covered valleys between dunes. In the SBDs, males are more mobile than females, and individuals generally have larger home ranges than other populations, possibly due to the habitat structure [48]. In the SBDs, lesser earless lizards move within vegetated areas, traveling around, rather than through, open, darkly colored cryptobiotic crust areas [48, pers. obs.]. Blanded lesser earless lizards at WSNP have comparatively longer limbs and a larger body size than adjacent populations of darker individuals [47]. Long limbs can improve sprint speeds, and WSNP blanded lesser earless lizards often sprint away from simulated predators [49].

WSNP has a lower abundance of potential predators of earless lizards than can be found in the surrounding Chihuahuan Desert, providing the blanded population with lower predation pressure than individuals in adjacent dark sand habitats [14,50]. Potential

predators in GUMO include roadrunners (*Geococcyx californianus*), loggerhead shrikes (*Lanius ludovicianus*), coachwhips (*Masticophis flagellum*), western diamondback rattlesnakes (*Crotalus atrox*), and coyotes (*Canis latrans*) [51]. In addition, long-nosed leopard lizards (*Gambelia wislizenii*) occur in the SBDs [pers. obs.] and are potential predators of lesser earless lizards. However, the extent of predation pressure on blanché lesser earless lizards at the SBDs is not known, as predator abundance surveys have not been systematically conducted there.

While surveying the SBDs, we observed many lesser earless lizards in flight, frequently moving away from us and into vegetation as surveyors approached. Lizards were wary and vigilant, stopping frequently or perching on vegetation to scan their surroundings, leading us to our first hypothesis, that in the presence of a predator, refuge access shapes escape behavior. As we never observed individuals escaping into burrows during our initial observations, we solely consider escape into vegetation as refuge-seeking behavior for this study. We predicted that individuals would adjust their movements relative to vegetation, with escaping lizards moving into large plants while fleeing a potential predator. Males and females used space on the study site differently [48] and varied in their reproductive roles, leading to our second hypothesis, that the movement patterns of escaping lizards (i.e., the number and length of moves) would vary with sex. Third, we hypothesized that movement patterns would vary based on vegetation, trial length, and experience. We predicted that the longer the pursuit (i.e., trial length), the longer the moves and the larger the plants used by escaping lizards. Furthermore, we predicted that lizards captured prior to escape trials (i.e., experienced) would be more wary, initiating escape more quickly (=longer FID) and escaping more readily (=shorter trial length) than individuals that were not captured and handled prior to their escape trial (i.e., inexperienced).

2. Materials and Methods

We surveyed the central 103 ha of the SBDs in GUMO, Hudspeth County, TX (31.920000° N, 104.989988° W, 1111 m asl; datum = WGS84) for blanché lesser earless lizards from 3 to 29 June 2022 while capturing and marking individuals for a separate study (Figure 1). We captured lizards with a lasso attached to the end of an extendable pole. We conducted escape trials of lesser earless lizards on 15–29 June 2022, examining escape behaviors at two levels of experience: experienced (i.e., previously handled and marked individuals, $n = 26$) and inexperienced (i.e., not handled or marked prior to trial, $n = 28$). We captured and measured inexperienced lizards after we completed their escape trials. Upon capture of unmarked lizards, we sexed, measured (snout–vent length (SVL) and tail length), and uniquely marked them on the dorsal base of their tail with non-toxic paint pens. We processed lizards used for escape trials near their capture location and released them at their capture site within 15 min. Lizards that were measured and marked as part of the separate study were handled in the same way as lizards used exclusively for escape trials but were released at their site of capture within 30 min. We did not conduct escape trials on experienced individuals until at least 3 days ($\bar{x} = 13$ days) after their release. We used individual lizards for only one escape trial.



Figure 1. Salt Basin Sand Dunes habitat with inset (**lower left**) of a marked, blanché lesser earless lizard from the study site.

Each trial involved a simulated predator (MMO), a scribe (DS), and an observer (KLU, DAE, MAE, or JBH). The simulated predator, wearing the same neutral clothing for every trial, positioned herself in full view of the lizard (i.e., unobstructed line of sight) and chose a starting position approximately 5 m away (accounting for vegetation and landscape contour) on level ground, perpendicular to the focal lizard's body. Prior to beginning trials, the simulated predator practiced and became proficient at maintaining a pace of 0.7 m/s, which she then used to approach lizards during trials. If the lizard was first observed on a dune face, the simulated predator waited until the animal moved onto level ground before starting the trial. During the trial, the scribe remained behind the simulated predator (ca. ≥ 10 m) and recorded the trial events (move length, move directionality, and use of vegetation) as dictated by the simulated predator (in a soft voice, so as not to disturb the lizards). We defined moves as forward motion of the lizard's body preceded and followed by a pause. The simulated predator categorized each move length as short (<0.5 m), medium (0.5–1 m), long (1–5 m), or run (>5 m) throughout the trial. The simulated predator practiced determining move lengths against known distances until she could consistently assign move lengths to the correct categories. The simulated predator also classified the ending location of each move (in vegetation or in the open) and noted move directionality when the lizard went up or down a dune face. We considered a plant to be used by the focal animal if a move was made during escape within 25 cm (=vegetation edge) or under (=in vegetation) the canopy of a plant. We also recorded when a focal lizard moved along the edge of a plant (=around). The simulated predator placed numbered pins on each plant along the escape path used by the lizard during its trial to indicate the sequence of vegetation visited. We recognized three possible ways trials could end (=trial outcome): (1) a 2 min time limit was reached, (2) the lizard moved out of sight for 10 s, or (3) the lizard was in vegetation and visible to the simulated predator but not moving for 10 s. A successful escape only included a lizard that moved out of sight (i.e., trial outcome 2). The scribe recorded the start time, the dictated movement sequences, the trial outcome, and the trial length. The observer timed and watched the trial to confirm the sequence of movements. After the completion of a trial, the simulated predator, observer, and scribe

retraced the movement sequence and the pinned vegetation to ensure accuracy. After the trial, we recorded flight initiation distance (FID), start distance (SD = the distance between lizard and simulated predator at the start of the trial), plant species identity, canopy size (longest length and the corresponding perpendicular width), substrate temperature at the lizard's start location (=lizard start temperature), and habitat type at the start location (sandy dune slope, dune with cryptobiotic crust, flat sand, or flat cryptobiotic crust). Plants we identified that were used by focal lizards were sage (*Artemisia filifolia*), soaptree yucca (*Yuca elata*), sand fiddleleaf (*Nama carnososa*), hairy crinklemat (*Tiliquilia hispidissima*), littleleaf rhatany (*Krameria erecta*), grass, and woody branches without foliage (categorized as "wood"). The grasses were non-reproductive, and we categorized them collectively rather than by individual species. Sage shrubs formed congregated patches along the sandy substrate and represented the most common vegetation type. Soaptree yucca, although less prevalent than sage, created a tall vertical structure used for cover. Grasses occurred widely in open spaces. Sand fiddleleaf, hairy crinklemat, and littleleaf rhatany were less prominent, generally scattered throughout the SBDs. Bare branches ("wood") were less common but were potential perching habitats for lizards. Sage, grass, and yucca were the most prominent vegetation across the study site.

2.1. Escape Analysis

We used a general linear model (GLM) to determine which of factors (categorical: start habitat, experience level, and sex; and covariate: substrate temperature) were influential for 3 escape measures (FID, number of moves, and number of plants visited) and trial length. For trial length, we additionally used the categorical variable: trial outcome. Model results were examined to assure normality and homoskedasticity. Tukey tests, with $p < 0.05$, were used for post hoc comparisons. We examined the relationship between trial length and move length using Pearson's correlation between the number of moves in a trial and the frequency with which different move lengths occurred. For examining the independence of categorical variables, we used a χ^2 -test, using the standardized residuals for interpretation. We also used chi-square tests to examine the sequence of move lengths in a trial, testing for independence of move length from one move to the next.

2.2. Habitat Use

We used Pearson correlation tests to assess the relationship between plant size, move length, and move frequency. To evaluate the role of vegetation characteristics on escape behavior, we focused on sage, the most commonly used plant during trials, assessing two aspects of size: length and width. We performed a binary logistic regression (logit link function) to examine if length, width, substrate temperature, and the number of moves within sage plants were influential in determining if a trial ended in a particular sage.

3. Results

We ran escape trials on 55 individuals ($n = 28$ females, 23 males, 4 uncaptured (sex unknown); Table 1). Most trials (62%) concluded with the lizard escaping ($n = 34$), 25% lasted the full 2 min ($n = 14$), and 13% ended due to lack of movement ($n = 7$). Trial outcome was not dependent on sex ($\chi^2 = 3.71$, $df = 2$, $p = 0.16$) or experience level ($\chi^2 = 0.68$, $df = 2$, $p = 0.71$).

Table 1. Summary statistics for escape trials (mean $\pm$ SE (range)).

	Mean $\pm$ SE (Range)
Start distance (cm)	509.3 $\pm$ 16.2 (165–755)
FID (cm)	133.2 $\pm$ 11.1 (5–385)

Table 1. Cont.

	Mean $\pm$ SE (Range)
Trial length (s)	79.34 $\pm$ 4.50 (23–120)
Trial moves (<i>n</i>)	14.80 $\pm$ 1.29 (1–39)

3.1. Escape Analysis

3.1.1. FID

FID was related to the habitat in which the trial began (GLM: $F_{5,42} = 3.44$, $p = 0.011$; Total Model: $R^2 = 31.81$; Table 2). FID was longest for individuals that began trials on wood (Figure 2) and significantly greater than escape trials beginning in grass, yucca, or sage (Figure 2; Table 3).

Table 2. ANOVA results (*F*-value, degrees of freedom (df), and *p*-value) from GLM testing the effect on FID of the substrate temperature at the start of a trial, the starting vegetation, sex of trial lizard, whether the tested lizard was captured before or after the trial (experience), how the trial ended (trial outcome, i.e., escape, time limit, or stopped moving), and the length of the trial. Significant *p*-values are in bold.

	FID			Trial Length			Number of Moves			Number of Plants		
Source	<i>F</i>	df	<i>p</i>	<i>F</i>	df	<i>p</i>	<i>F</i>	df	<i>p</i>	<i>F</i>	df	<i>p</i>
Start °C	2.89	1.41	0.097	0.19	1.43	0.665	1.21	1.44	0.277	0.05	1.43	0.830
Start habitat	3.44	5.41	0.011	1.59	5.43	0.183	2.11	5.44	0.083	4.60	5.43	0.002
Sex	0.11	1.41	0.742	3.01	1.43	0.090	1.89	1.44	0.176	1.12	1.43	0.295
Experience	1.09	1.41	0.302	0.12	1.43	0.729	0.36	1.44	0.552	0.10	1.43	0.751
Trial outcome	--	--	--	21.96	2.43	<0.0001	--	--	--	--	--	--
Trial length (s)	--	--	--	--	--	--	87.98	1.44	<0.0001	7.28	1.43	0.010

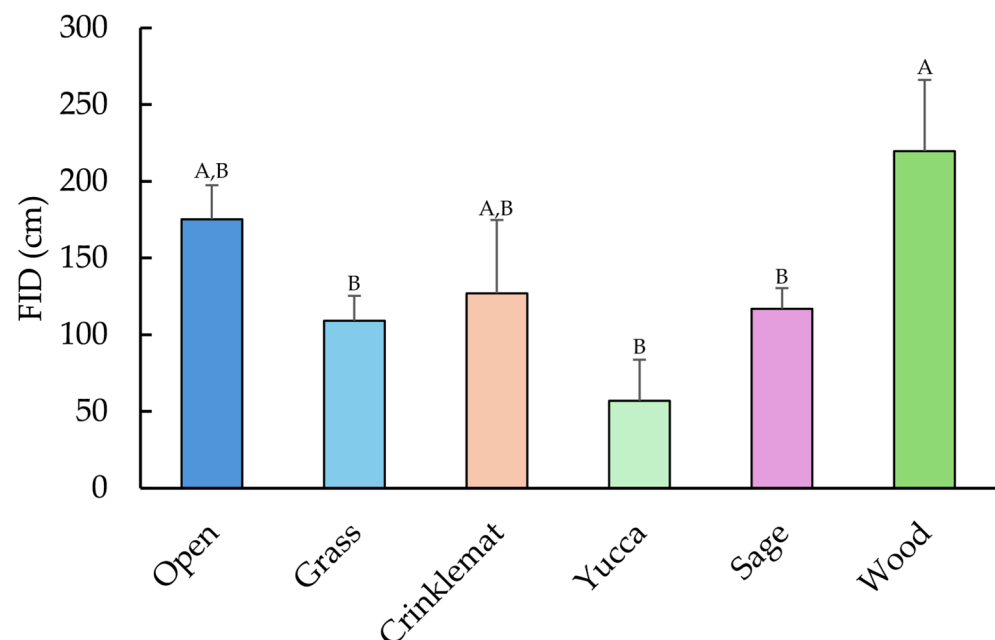


Figure 2. FID lengths by starting habitat. Habitats with unlike letters are significantly different.

Start habitat was independent of sex ($\chi^2 = 5.67$, $df = 5$, $p = 0.339$) and experience level ($\chi^2 = 3.024$, $df = 5$, $p = 0.696$). Substrate temperature at the start of escape trials varied by habitat ($F_{5,53} = 4.64$, $p = 0.001$, $R^2 = 30.44$), with the substrate under wood having a higher temperature than the substrate under grass and sage (Table 3).

Table 3. FID (*n*, mean, and SE), substrate temperature, and number of habitat items (“vegetation”) used during escape sequences for each starting habitat. Values within a column that have unlike subscripts are significantly different.

Start Habitat		FID (cm)		Substrate Temp. (°C)	Vegetation (<i>n</i>)
	<i>n</i>	Mean	SE		
Crinklemat	5	127.0 _{A,B}	47.8	37.2 _{A,B}	13.6 _A
Grass	13	109.2 _B	16.1	33.33 _B	6.62 _{A,B}
Open	7	175.3 _{A,B}	22.1	37.71 _{A,B}	4.71 _{A,B}
Wood	7	219.6 _A	46.4	45.69 _A	4.0 _B
Sage	20	116.9 _B	13.5	32.73 _B	3.5 _B
Yucca	3	57.0 _B	26.6	38.58 _{A,B}	2.0 _{A,B}

3.1.2. Trial Characteristics

Trial length was significantly related to trial outcome (GLM: $F_{2,43} = 21.96$, $p < 0.001$; Total Model: $R^2 = 58.53$; Table 2). Trials where focal lizards moved out of sight were shorter than trials lasting the full 2 min or that ended with the lizard stopping movement. In addition, the number of moves in an escape sequence was related to trial length (GLM: $F_{1,44} = 87.98$, $p < 0.001$; Total Model: $R^2 = 75.35$; Table 2). Longer escape trials were composed of more moves (Table 2).

We evaluated move lengths for first moves ($n = 59$) up to twentieth moves ($n = 19$), corresponding to the number of moves in the longest escape sequences with a sufficient sample size for analysis. As trial length increased, the number of short (Pearson’s correlation: $r = 0.658$, $p < 0.001$), medium ($r = 0.626$, $p < 0.001$), and long moves ($r = 0.481$, $p < 0.001$) increased, but runs were not significant ($r = -0.138$, $p = 0.296$). Likewise, the number of short ($r = 0.645$, $p < 0.001$), medium ($r = 0.612$, $p < 0.001$), and long moves ($r = 0.781$, $p < 0.001$) also increased with the total number of moves, but runs were not significant ($r = -0.084$, $p = 0.528$). Within a trial, the number of long moves was correlated with the number of medium moves ($r = 0.366$, $p = 0.004$), but no other pairwise combination of moves was significant (long-short: $p = 0.441$, run-short: $p = 0.277$, run-medium: $p = 0.470$, run-long: $p = 0.513$). The distribution of move lengths was influenced by sex ($\chi^2 = 12.428$, $df = 3$, $p = 0.006$; Figure 3), with males making fewer short and more long moves than expected, and females employing more small and fewer long moves than expected. During escape trials, sequences of short–short and long–long moves occurred at a higher-than-expected frequency ($\chi^2 = 160.4$, $df = 4$, $p < 0.001$). As an escape sequence progressed, the proportion of move lengths changed: small moves became more common ($r = 0.500$, $p = 0.025$), while long moves became less common ($r = -0.479$, $p = 0.032$).

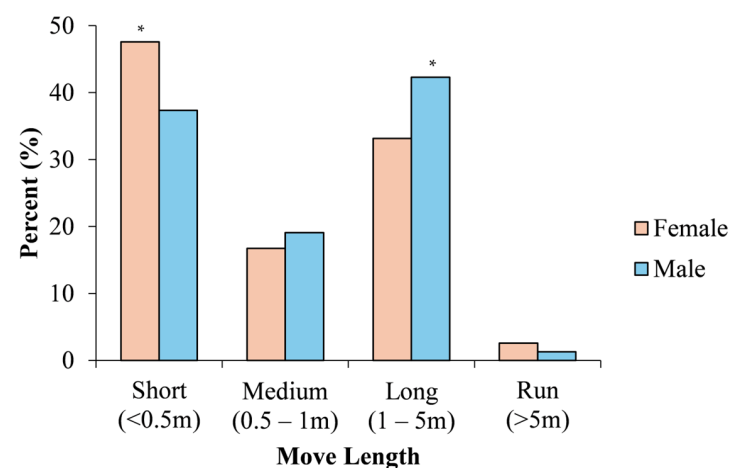


Figure 3. Sex-based distribution of move lengths. * = Significant differences between the sexes.

3.2. Vegetation Use

3.2.1. Number of Plants Visited

During escape trials, focal individuals entered a mean of 5.2 ± 0.7 unique plants (range = 1–24 plants/trial). The total number of unique plants visited/trial was significantly related to trial length (GLM: $F_{1,43} = 7.28$, $p = 0.010$, Total Model: $R^2 = 45.95$) and start habitat ($F_{5,43} = 4.60$, $p = 0.002$; Table 2). During longer trials, lizards used more plants. In addition, during trials that started in sage bushes or wood, fewer plants were used than by lizards starting in crinklemat (Table 3; Figure 4). For the seven plant types visited most frequently during escape trials, sex was not related to plant species ($\chi^2 = 5.664$, $df = 6$, $p = 0.462$).

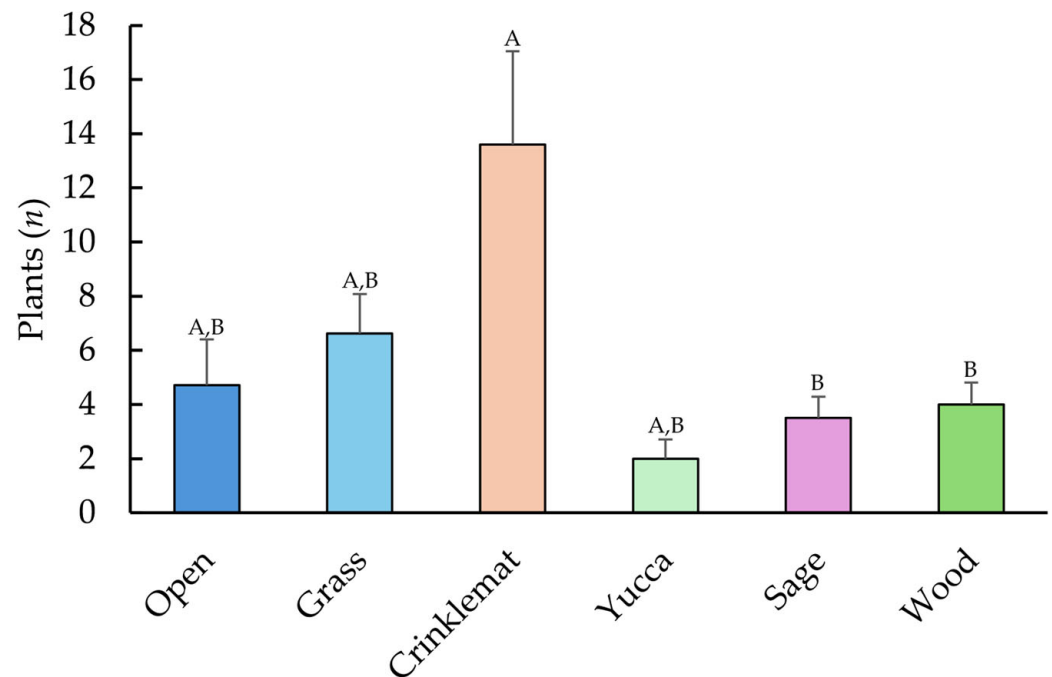


Figure 4. Mean of the number of habitat items (“plants”) visited by individuals during escape trials. Habitats with unlike letters are significantly different.

3.2.2. Sage Use

Sage played an increasingly important role as escape sequences progressed, with 71% of the trials ending in sage, while only 39% of escape trials began in sage (Fisher exact: $p = 0.001$). The number of moves within a single sage bush was quite variable ($\bar{x} = 3.4 \pm 0.5$, range = 0–23 moves/sage (n.b., 0 moves = plant entered but no moves within the plant)). The number of moves in an individual sage bush was positively correlated with the plant’s size (length: $r = 0.34$, $p < 0.001$; width: $r = 0.32$, $p = 0.001$; area: $r = 0.26$, $p = 0.006$; Table 4). Move lengths also were positively correlated with the size of a sage bush used during an escape (Table 5).

Table 4. Summary of the characteristics of the sage plants ($n = 110$) visited during escape trials by lesser earless lizards.

Variable	Mean $\pm$ SE	Range
Length (cm)	311 ± 18	(30–1149)
Width (cm)	196 ± 9	(25–527)
Area (length $\times$ width) (m ²)	7.8 ± 0.8	(0.5–60.6)

Table 5. Pearson’s correlations (r (p)) between size of a sage bush used during an escape (width and length) and the number of short, medium, and long moves made in that bush during the escape sequence. Runs never occurred within a sage bush.

Move Length	Sage Bush	
	Width	Length
Short	0.15 ($p = 0.106$)	0.21 ($p = 0.026$)
Medium	0.43 ($p < 0.001$)	0.31 ($p = 0.001$)
Long	0.27 ($p = 0.004$)	0.35 ($p < 0.001$)

Lizards ended their escape trials in 37 of the 110 sage bushes they entered—~34% of the individual sage bushes served as the final refuge for escaping lizards. Of the 23 lizards who started trials in a sage, 9 had trials that ended in the same sage. The width of a particular sage and number of moves an escaping individual made within that same sage were significant predictors of whether the trial ended in that same sage (binary logistic regression: width, $\chi^2 = 4.56$, $df = 1$, $p = 0.033$; number of moves, $\chi^2 = 6.84$, $df = 1$, $p = 0.009$). Wider sages and longer trials were indications that a trial would end in a given sage. When examining whether a lizard escaped into a particular sage during its escape sequence, plant width acted as a significant factor (binary logistic regression: width, $\chi^2 = 5.46$, $df = 1$, $p = 0.020$), with escape more likely in wider plants.

4. Discussion

Our hypothesis that lesser earless lizards would vary their escape sequences in response to refuge access was supported. When serving as refuges, vegetation, particularly sage, shaped escape behaviors at the SBDs. Lizards adjust their escape behaviors based on refuge proximity and predator risk [24,52], and their escape sequences can be influenced by habitat structure, resource availability, and social dynamics [53,54]. Lesser earless lizards made use of large sages during escapes and varied their escape sequences relative to vegetation. Escaping individuals avoided the simulated predator by moving deeper into or among a sage plant, resulting in more moves and increasing move lengths with increasing sage bush size (Table 5).

We postulate that sage usage by lesser earless lizards in the SBDs might be based on an optimal combination of cover and accessibility during escape. The refuge-use theory posits that prey select refuges that minimize predation risk and optimize safety [4,55], which is in accordance with the behavior we observed by SBD lesser earless lizards. Sage bushes with a larger canopy (i.e., width) were particularly important during escape sequences, with lizards often ending trials in them. The number and length of moves within sage bushes also increased with bush size, raising the possibility that larger bushes were perceived as more secure refuges that facilitated more extensive movement. Their greater reliance on sage relative to other available plant species, particularly later in escape sequences, coupled with the predictive role of the width of a sage bush’s canopy to the escape trial outcome indicated the importance of vegetation structure for effective predator evasion. However, other factors beyond the scope of our study could account for sage use by lesser earless lizards. An analysis of the size and relative proportions of available vegetation is needed to definitively determine the importance of sage-secure refuges for lesser earless lizards. In addition, sage bushes could provide direct benefits, through their effects on microclimate (i.e., providing thermoregulatory opportunities) [56], or indirect benefits, through their role as a forage plant (i.e., providing feeding resources) [57]. Further study on the aspects of habitat structure that contribute to refuges for lesser earless lizards and are important to their movement and ecological stability are merited.

In our study, FIDs varied with starting habitat, being longest for lizards starting on wood (Figure 2). In open habitats where wood can serve as an available perch, lizards often have longer FIDs, possibly due to limited cover, requiring them to flee farther to reach safety [58,59]. The longer FIDs for lizards beginning on wood also could be related to the warmer substrate temperatures we recorded at the start of those escape trials compared to substrate temperatures for lizards starting at other refuges (Table 3), as escape behaviors can vary with the thermal properties of the environment and perceived predation risk [10,34]. Lizards often balance the thermal costs of seeking refuge against the risk of predation, as cooler habitats are associated with lower body temperatures [34,60]. When deciding when to flee and when to emerge from hiding, lizards rely on several factors, including the speed at which a predator approaches and distance to the nearest refuge [10]. Furthermore, lower body temperatures can increase FID due to decreased agility, potentially requiring earlier flight initiation [33]. Although substrate temperatures for wood habitats were often warmer (Table 3), the increased FID we observed in lizards starting on wood could be tied to a heightened perception of risk associated with the visibility of wood perches. Wood could offer fewer immediate hiding spots compared to grass or sage, increasing the time a lizard might spend assessing its environment before fleeing. Lizards also showed flexible movement patterns, with starting plant type influencing the number of plants visited during flight (Table 3). Larger vegetation types were associated with shorter FIDs, as lizards might have relied on nearby hiding spots or camouflage instead of making long escapes [61,62].

Our second hypothesis proposed that the movement patterns of escaping lizards (i.e., the number and length of moves) would vary with sex, vegetation, trial length, and experience, which was partially supported. The distribution of move lengths showed some association with sex (Figure 3). We predicted that longer pursuits (i.e., greater trial length) would result in longer moves and use of larger plants as refuges, and our prediction was mostly supported—small, medium, and long moves increased with trial length, and larger sage plants were the most common end refuge. Furthermore, we predicted that experienced individuals would have longer FIDs and shorter pursuit times (i.e., trial lengths), and would more rapidly retreat into a refuge. However, contrary to our expectations, experience had no detectable relationship with any escape variables.

Consistent with sex-based differences in home range previously reported for lesser earless lizards [48], males exhibited longer movement lengths than females (Figure 3). However, unlike patterns described in other lizard species [7,54,63], we did not detect significant sex differences in escape responses or habitat use. Sex-based effects were restricted to step-by-step movement patterns rather than broader anti-predator or space-use behaviors, and escape tactics might be more strongly shaped by ecological context than by sex.

Our study has certain limitations. Our vegetation analysis primarily focused on plant type and structural size. However, more detailed assessments of canopy density, thermal buffering capacity, or visibility obstruction could likely yield valuable ecological context. Future research incorporating predation activity and habitat complexity data would aid in clarifying the mechanisms underlying escape by lesser earless lizards.

Author Contributions: Conceptualization, D.A.E., D.S., J.B.H., K.L.U., M.A.E. and M.M.O.; methodology, D.A.E., D.S., J.B.H., K.L.U., M.A.E. and M.M.O.; validation, D.A.E., D.S., K.L.U. and M.M.O.; formal analysis, D.A.E., D.S., K.L.U. and M.M.O.; investigation, D.A.E., D.S., J.B.H., K.L.U., M.A.E., M.M.O. and T.G.L.; resources, D.A.E. and M.A.E.; data curation, D.A.E.; writing—original draft preparation, D.A.E., D.S., K.L.U., M.A.E. and M.M.O.; writing—review and editing, D.A.E., D.S., K.L.U., M.A.E. and T.G.L.; visualization, D.A.E. and D.S.; supervision, D.A.E. and M.A.E.; project

administration, D.A.E. and M.A.E.; funding acquisition, D.A.E. and M.A.E. All authors have read and agreed to the published version of the manuscript.

Funding: Funding for this project was provided by the Western National Parks Association (grant no. WNPA 22-04 GUMO) and Erell Institute.

Institutional Review Board Statement: Lizards were captured and handled in accordance with the guidelines for the ethical treatment of animals by the Animal Behavior Society and the American Society of Ichthyologists and Herpetologists' Animal Care and Use Committee, under the approval of Erell Institute's Animal Care and Use Committee (IACUC proposal no. 2022-02; approved 10 March 2022).

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors on request.

Acknowledgments: We thank the Guadalupe Mountains National Park for encouraging our research and providing us access to the Salt Basin Dunes. Drew Dittmer provided invaluable guidance concerning working in the Salt Basin Dunes.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

FID	Flight initiation distance: distance between lizard and simulated predator when the lizard initially flees
GLM	General linear model
GUMO	Guadalupe Mountains National Park, Texas, USA
SBDs	Salt Basin Dunes, Texas, USA
SD	Start distance: distance between lizard and simulated predator at the beginning of a trial
SVL	Snout–vent length: a measure of lizard size (length from anterior edge of the snout to the posterior edge of the cloaca)
WSNP	White Sands National Park, New Mexico, USA

References

1. Caro, T. *Antipredator Defenses in Birds and Mammals*; University of Chicago Press: Chicago, IL, USA, 2005.
2. Lima, S.L.; Dill, L.M. Behavioral decisions made under the risk of predation: A review and prospectus. *Can. J. Zool.* **1990**, *68*, 619–640. [[CrossRef](#)]
3. Ydenberg, R.C.; Dill, L.M. The economics of fleeing from predators. *Adv. Study Behav.* **1986**, *16*, 229–249.
4. Cooper, W.E.; Frederick, W.G. Optimal flight initiation distance. *J. Theor. Biol.* **2007**, *244*, 59–67. [[CrossRef](#)]
5. Cooper, W.E., Jr.; Hawlena, D.; Pérez-Mellado, V. Effects of predation risk factors on escape behavior by Balearic lizards (*Podarcis lilfordi*) in relation to optimal escape theory. *Amphib. Reptil.* **2009**, *30*, 99–110. [[CrossRef](#)]
6. Martín, J.; López, P. Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammodromus algirus*. *Ethology* **1999**, *105*, 439–447. [[CrossRef](#)]
7. Cooper, W.E., Jr. Age, sex and escape behavior in the striped plateau lizard (*Sceloporus virgatus*) and the mountain spiny lizard (*S. jarrovi*), with a review of age and sex effects on escape by lizards. *Behaviour* **2011**, *148*, 1215–1238. [[CrossRef](#)]
8. Martín, J.; López, P. Thermal constraints of refuge use by Schreiber's green lizards, *Lacerta schreiberi*. *Behaviour* **2010**, *147*, 275–284.
9. Cooper, W.E., Jr.; Pérez-Mellado, V.; Baird, T.A.; Caldwell, J.P.; Vitt, L.J. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards *Cnemidophorus murinus*. *Behav. Ecol.* **2003**, *14*, 288–293. [[CrossRef](#)]
10. Martín, J.; López, P. Wall lizards modulate refuge use through continuous assessment of predation risk level. *Ethology* **2005**, *111*, 207–219. [[CrossRef](#)]
11. Braun, C.A.; Baird, T.A.; LeBeau, J.K. Influence of substrate temperature and directness of approach on the escape responses of juvenile collared lizards. *Herpetologica* **2010**, *66*, 418–424. [[CrossRef](#)]
12. Kacoliris, F.P.; Guerrero, E.; Molinari, A.; Moyano, B.; Rafael, A. Run to shelter or bury into the sand? Factors affecting escape behavior decisions in Argentinian sand dune lizards (*Liolaemus multimaculatus*). *Herpetol. J.* **2009**, *19*, 213–216.

13. Chhoumi, O.; Eifler, M.A.; Orton, M.M.; Eifler, D.A.; Selmi, S. Multiple vs. single predator effects: Differing experimental responses by the spotted fringe-fingered lizard (*Acanthodactylus maculatus*) facing aerial and terrestrial predators. *J. Ethol.* **2024**, *43*, 31–38. [\[CrossRef\]](#)
14. Robertson, J.M.; Hoversten, K.; Gründler, M.; Poorten, T.J.; Hews, D.K.; Rosenblum, E.B. Colonization of novel White Sands habitat is associated with changes in lizard anti-predator behavior. *Biol. J. Linn. Soc.* **2011**, *103*, 657–667. [\[CrossRef\]](#)
15. Stankowich, T.; Blumstein, D.T. Fear in animals: A meta-analysis and review of risk assessment. *Proc. R. Soc. B* **2005**, *272*, 2627–2634. [\[CrossRef\]](#) [\[PubMed\]](#)
16. Eifler, D.A.; Eifler, M.A. Escape tactics in the lizard *Meroles cuneirostris*. *Amphib. Reptil.* **2014**, *35*, 383–389. [\[CrossRef\]](#)
17. Eifler, D.A.; Eifler, M.A.; Garrison, G.E.; Grotbeck, V.L. Escape angles for solitary animals and groups of the lizard *Pholidoscelis fuscatus*. *Ethol. Ecol. Evol.* **2022**, *35*, 125–133. [\[CrossRef\]](#)
18. Cooper, W.E., Jr. Pursuit deterrence varies with predation risks affecting escape behaviour in the lizard *Callisaurus draconoides*. *Anim. Behav.* **2010**, *80*, 249–256. [\[CrossRef\]](#)
19. Burger, J.; Gochfield, M.; Murray, B.G. Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). *J. Comp. Psychol.* **1992**, *106*, 97–101. [\[CrossRef\]](#)
20. Hemmi, J.M. Predator avoidance in fiddler crabs. 1. Escape decisions in relation to the risk of predation. *Anim. Behav.* **2005**, *69*, 603–614. [\[CrossRef\]](#)
21. Cooper, W.E., Jr. Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behav. Ecol. Sociobiol.* **2009**, *63*, 1765–1771. [\[CrossRef\]](#)
22. Samia, D.S.M.; Blumstein, D.T.; Stankowich, T.; Cooper, W.E., Jr. Fifty years of chasing lizards: New insights advance optimal escape theory. *Biol. Rev.* **2016**, *91*, 349–366. [\[CrossRef\]](#)
23. Liu, E.F.; Eifler, M.A.; Buchanan, C.A.; Gilbert Smith, S.; Eifler, D.A. Escape by juvenile Little Striped Whiptails (*Aspidoscelis inornatus* Baird, 1859) in response to predator approach speed (Lacertilia: Teiidae). *Herpetol. Notes* **2021**, *14*, 479–483.
24. Martín, J.; López, P. Influence of habitat structure on the escape tactics of the lizard *Psammmodromus algerius*. *Can. J. Zool.* **1995**, *73*, 129–132. [\[CrossRef\]](#)
25. Forsman, A. Temperature influence on escape behaviour in two species of pygmy grasshoppers. *Ecoscience* **1999**, *6*, 35–40. [\[CrossRef\]](#)
26. Özbilgin, H.; Wardle, C.S. Effect of seasonal temperature changes on the escape behaviour of haddock, *Melanogrammus aeglefinus*, from the codend. *Fish. Res.* **2002**, *58*, 323–331. [\[CrossRef\]](#)
27. Stankowich, T.; Coss, R.G. Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behav. Ecol.* **2007**, *18*, 358–367. [\[CrossRef\]](#)
28. Nahin, P.J. *Chases and Escapes: The Mathematics of Pursuit and Evasion*; Princeton University Press: Princeton, NJ, USA, 2007.
29. Cresswell, W. Escape responses by redshanks, *Tringa tetanus*, on attack by avian predators. *Anim. Behav.* **1993**, *46*, 609–611. [\[CrossRef\]](#)
30. Edut, S.; Eilam, D. Protean behavior under barn-owl attack: Voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. *Behav. Brain Res.* **2004**, *155*, 207–216. [\[CrossRef\]](#)
31. Martín, J.; López, P. Hiding time in refuge. In *Escaping from Predators: An Integrative View of Escape Decisions*; Cooper, W.E., Jr., Blumstein, D.T., Eds.; Cambridge University Press: Cambridge, UK, 2015; pp. 227–262.
32. Cooper, W.E., Jr.; Van Wyk, J.H.; Mouton Le, F.P.; Mouton, N. Incompletely protective refuges: Selection and associated defenses by a lizard, *Cordylus cordylus* (Squamata: Cordylidae). *Ethology* **1999**, *105*, 687–700. [\[CrossRef\]](#)
33. Kerr, G.; Bull, M.C.; Burzacott, D. Refuge sites used by the scincid lizard *Tiliqua rugosa*. *Austral Ecol.* **2003**, *28*, 152–160. [\[CrossRef\]](#)
34. Martín, J.; López, P. Ontogenetic variation in antipredator behavior of Iberian rock lizards (*Lacerta monticola*): Effects of body-size-dependent thermal exchange rates and costs of refuge use. *Can. J. Zool.* **2003**, *81*, 1131–1137. [\[CrossRef\]](#)
35. Martín, J.; López, P. Costs of refuge use affect escape decisions of Iberian rock lizards *Lacerta monticola*. *Ethology* **2000**, *106*, 483–492. [\[CrossRef\]](#)
36. Cooper, W.E., Jr. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *J. Can. Zool.* **1997**, *75*, 943–947. [\[CrossRef\]](#)
37. Eifler, D.A. *Egernia cunninghami* (Cunningham's skink): Escape behavior. *Herpetol. Rev.* **2001**, *30*, 40.
38. Stapley, J. Differential avoidance of snake odours by a lizard: Evidence for prioritized avoidance based on risk. *Ethology* **2003**, *109*, 785–796. [\[CrossRef\]](#)
39. Amo, L.; López, P.; Martín, J. Trade-offs in the choice of refuges by common wall lizards: Do thermal costs affect preferences for predator free refuges? *Can. J. Zool.* **2004**, *82*, 897–901. [\[CrossRef\]](#)
40. Rosenblum, E.B.; Burkett, D.; Blaine, R. Common lesser earless lizard: *Holbrookia maculata* Girard, 1851. In *Lizards of the American Southwest*; Jones, L.L.C., Lovich, R.E., Eds.; Rio Nuevo Publishers: Tucson, AZ, USA, 2009; pp. 154–157.
41. Rosenblum, E.B.; Harmon, L.J. Same same but different: Replicated ecological speciation at White Sands. *Evolution* **2011**, *65*, 946–960. [\[CrossRef\]](#)

42. Walkup, D.K.; Leavitt, D.J.; Fitzgerald, L.A. Effects of habitat fragmentation on population structure of dune-dwelling lizards. *Ecosphere* **2017**, *8*, 01729. [\[CrossRef\]](#)
43. Hager, S.B. Microhabitat use and activity patterns of *Holbrookia maculata* and *Sceloporus undulatus* at White Sands National Monument, New Mexico. *J. Herpetol.* **2001**, *35*, 326–330. [\[CrossRef\]](#)
44. Hager, S.B. Quantification of body coloration for the lesser earless lizard, *Holbrookia maculata*: Evidence for interpopulational differences. *Southwest. Nat.* **2002**, *47*, 299–307. [\[CrossRef\]](#)
45. Rosenblum, E.B.; Rompler, H.; Schoneberg, T.; Hoekstra, H.E. Molecular and functional basis of phenotypic convergence in white lizards at White Sands. *Proc. Natl. Acad. Sci. USA* **2009**, *107*, 2113–2117. [\[CrossRef\]](#) [\[PubMed\]](#)
46. Des Roches, S.; Brinkmeyer, M.S.; Harmon, L.J.; Rosenblum, E.B. Ecological release and directional change in White Sands lizard trophic ecomorphology. *Evol. Ecol.* **2015**, *29*, 1–16. [\[CrossRef\]](#)
47. Laurentino, T.G.; Dittmer, D.E.; Grundler, M.R.; Pina-Martins, F.; Haddock, J.; Hibbitts, T.J.; Rosenblum, E.B. Repeated evolution of blanched coloration in a lizard across independent white-sand habitats. *Ecol. Evol.* **2022**, *12*, 9555. [\[CrossRef\]](#)
48. Orton, M.M.; Eifler, M.A.; Utsumi, K.L.; Laurentino, T.G.; Siddiqui, D.; Haddock, J.B.; Quock, R.; Eifler, D.A. *Holbrookia maculata* space use in the Salt Basin Dunes of the Guadalupe Mountains National Park. *Herpetol. Rev.* **2024**, *55*, 7–10.
49. Des Roches, S.; Torresdal, J.; Morgan, T.W.; Harmon, L.J.; Rosenblum, E.B. Beyond black and white: Divergent behaviour and performance in three rapidly evolving lizard species at White Sands. *Biol. J. Linn. Soc.* **2014**, *111*, 169–182. [\[CrossRef\]](#)
50. Des Roches, S.; Robertson, J.M.; Harmon, L.J.; Rosenblum, E.B. Ecological release in White Sands lizards. *Ecol. Evol.* **2011**, *1*, 571–578. [\[CrossRef\]](#)
51. Genoways, H.H.; Baker, R.J.; Cornely, J.E. Mammals of the Guadalupe Mountains National Park, Texas. *Mammal. Pap. Univ. Neb. State Mus.* **1975**, *114*, 271–332.
52. Wagner, E.A.; Zani, P.A. Escape behavior of Side-blotched Lizards (*Uta stansburiana*) in response to model predators. *Can. J. Zool.* **2017**, *95*, 965–973. [\[CrossRef\]](#)
53. Rodríguez-Prieto, I.; Martín, J.; Fernández-Juricic, E. Habituation to Low-Risk Predators Improves Body Condition in Lizards. *Behav. Ecol. Sociobiol.* **2010**, *64*, 1937–1945. [\[CrossRef\]](#)
54. Domínguez-López, M.E.; Diego-Rasilla, F.J.; Ortega-León, A.M. Effects of sex and microhabitat structure on escape behaviour in the diurnal gecko *Gonatodes albogularis*. *Anim. Biol.* **2016**, *66*, 31–47. [\[CrossRef\]](#)
55. Cooper, W.E., Jr.; Pérez-Mellado, V. Historical influence of predation pressure on escape by *Podarcis* lizards in the Balearic Islands. *Biol. J. Linn. Soc.* **2012**, *107*, 254–268. [\[CrossRef\]](#)
56. Yu, M.H.; Ding, G.D.; Gao, G.L.; Sun, B.P.; Zhao, Y.Y.; Wan, L.; Wang, D.Y.; Gui, Z.Y. How the plant temperature links to the air temperature in the desert plant *Artemisia ordosica*. *Sci. Rep.* **2015**, *5*, 12889. [\[CrossRef\]](#) [\[PubMed\]](#)
57. Wambolt, C.L.; Frisina, M.R.; Knapp, S.J.; Frisina, R.M. Preference of mule deer for big sagebrush taxa. *J. Range Manag.* **1996**, *49*, 499–503. [\[CrossRef\]](#)
58. Biaggini, M.; Berti, R.; Corti, C. Different habitats, different pressures? Analysis of escape behaviour and ectoparasite load in *Podarcis sicula* (Lacertidae) populations in different agricultural habitats. *Amphib. Reptil.* **2009**, *30*, 453–461. [\[CrossRef\]](#)
59. McBrayer, L.D.; Parker, S.E. Variation in habitat management alters risk aversion behavior in lizards. *Behav. Ecol. Sociobiol.* **2018**, *72*, 149. [\[CrossRef\]](#)
60. Eifler, D.A.; Dittmer, D.E.; Dick, L.; Rowe, B.; Johnson, J.J.; Stanley, D.R.; Eifler, M.A. Differences in habitat use, thermal ecology, and behavior of the semiaquatic lizard *Anolis aquaticus* at a high- and low-elevation site. *Diversity* **2025**, *17*, 673. [\[CrossRef\]](#)
61. Doherty, T.S.; Fist, C.N.; Driscoll, D.A. Animal movement varies with resource availability, landscape configuration and body size: A conceptual model and empirical example. *Landsc. Ecol.* **2019**, *34*, 603–614. [\[CrossRef\]](#)
62. Morelli, F.; Mikula, P.; Blumstein, D.T.; Díaz, M.; Markó, G.; Jokimäki, J.; Kaisanlahti-Jokimäki, M.; Floigl, K.; Abou Zeid, F.; Siretckaia, A.; et al. Flight initiation distance and refuge in urban birds. *Sci. Total Environ.* **2022**, *842*, 156939. [\[CrossRef\]](#)
63. Tryban, M.E.; Utsumi, K.L.; Olson, C.N.; Yang, J.L.; Reynolds, H.; Eifler, M.A.; Eifler, D.A. Sex-based variation in behavior for the little striped whiptail (*Aspidoscelis inornatus*). *Southwest. Nat.* **2024**, *68*, 112–120. [\[CrossRef\]](#)

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.