

DO POLYMORPHIC FEMALE BROWN ANOLES (*ANOLIS SAGREI*) DIFFER IN SPRINT SPEED OR ESCAPE BEHAVIOR?

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ABSTRACT: The Brown Anole (*Anolis sagrei*) is a polymorphic species, with females often exhibiting one of three distinct pattern morphs. Efforts to correlate female-limited pattern polymorphism in anoles to ecological or physiological factors have largely been unsuccessful, with such correlations being either inconsistent among species or among populations of a single species. To test the hypothesis that morph types would differ in their response to putative predators, we observed escape behavior in 84 female *A. sagrei* from Cape Eleuthera (Eleuthera, Bahamas) and tested 103 females for sprint speed. We found differences between morph types in hindlimb span and perch height. Differences in sprint speed were not significant, nor did morphs differ in escape responses. We suggest further studies to determine whether differences between morphs in hindlimb span are genetic or plastic, and, if plastic, what factor might be responsible. We conclude that perching at different heights could be selectively advantageous for different morph types, and that differences among individuals in sprint speed are largely consequences of hindlimb length. Because morphs in this population did not differ in escape responses, we suggest that different dorsal patterns are not linked to specific behaviors that could reduce detection by a potential predator.

Key words: Antipredator response; Bahamas; Dactyloidae; Female-limited pattern polymorphism

INDIVIDUALS within a population frequently exhibit multiple discrete phenotypes (e.g., Brito da Cunha, 1949; Lowther, 1961) that often vary in at least some characters related to survival, such as size, behavior, or even immune responses (e.g., Hover, 1985; Snorrason et al., 1994; Galeotti and Sacchi, 2003). Visible pattern variations are common especially in species that are exposed to avian predation (Stamps and Gon, 1983). In some species, polymorphism is limited to one sex. This kind of variation is much more commonly seen in females, and when males do not exhibit the same pattern morphs, the condition is known as female-limited pattern polymorphism (FPP; Stamps and Gon, 1983). FPP has been observed in many invertebrates (e.g., butterflies, spiders, crustaceans) and in some vertebrates (frogs, salamanders, snakes, lizards; Stamps and Gon, 1983).

Schoener and Schoener (1976) described FPP in Brown Anoles (*Anolis sagrei*) and associated it with vegetation types and perch diameters, but this topic was not revisited in *Anolis* until Calsbeek et al. (2008) initiated a

series of studies. Female *A. sagrei* near Cape Eleuthera, Eleuthera Island, Bahamas, fall fairly neatly into three previously defined categories (e.g., Cox and Calsbeek, 2011; Fig. 1). Diamond morphs have a series of nearly perfect middorsal diamonds; this pattern can also be viewed as two matched sets of paramedian triangles aligned along the middorsal line. Striped (also called bar) morphs have a single broad middorsal band or two thin lines on either side of the middorsal stripe. The diamond-bar morph includes lizards with patterns incorporating elements of both other morphs. Calsbeek et al. (2008) found that morph types in *A. sagrei* are heritable and are probably controlled by two loci (Calsbeek et al., 2010). The same patterns are not observed in males, with the exception that some juvenile males exhibit a striped pattern. Male anoles are rarely the more patterned sex, although a few exceptions have been documented (Losos, 2009).

FPP originated in West Indian anoles nearly 20 million years ago and has arisen independently several times from an ancestral absence (Paemelaere, 2010; Paemelaere et al., 2011a). Generally, mainland and trunk-perching species of anoles are more likely to exhibit FPP (Paemelaere, 2010; Paemelaere et al., 2011a).

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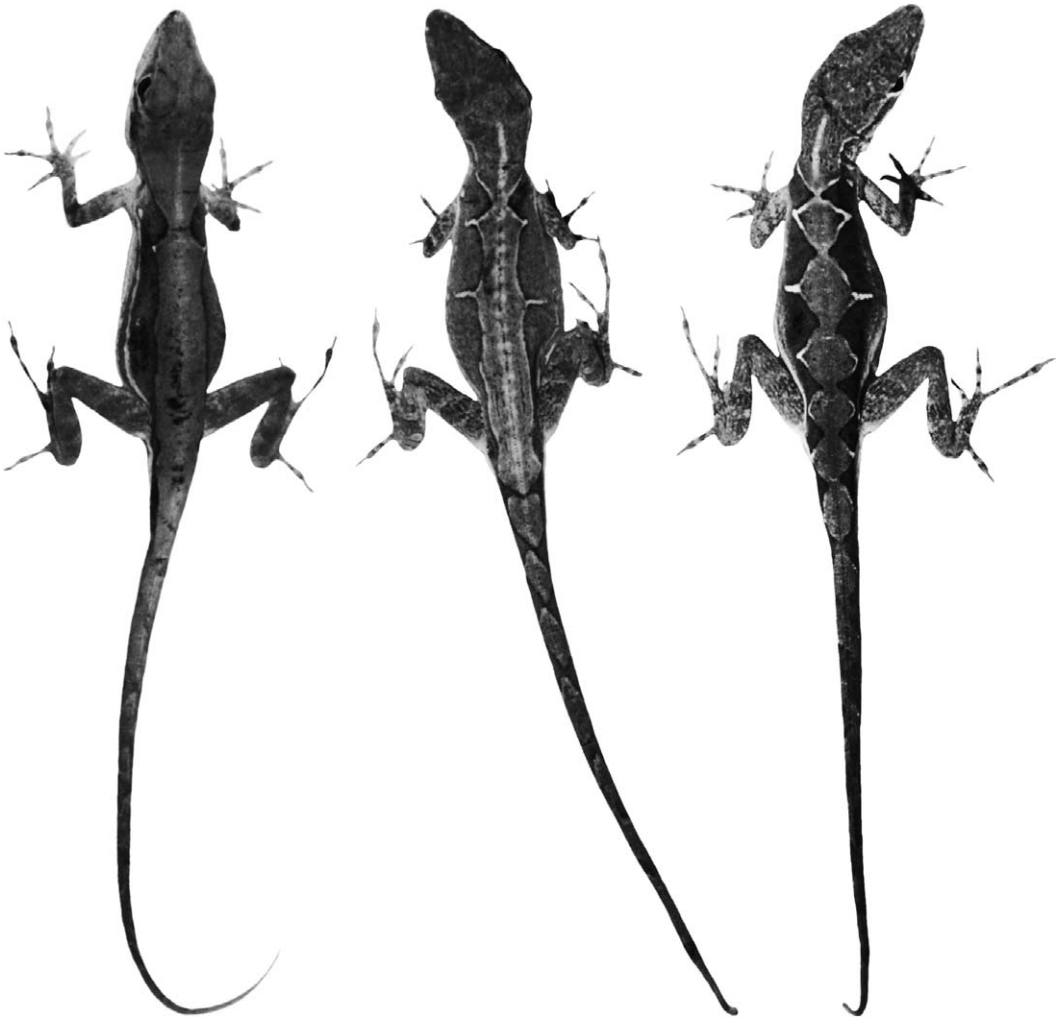


FIG. 1.—Female *Anolis sagrei* on Eleuthera are grouped into three categories based on differences in dorsal patterns. Left to right, the individuals above represent “striped” (= “bar”), “diamond-bar,” and “diamond” morphs.

The evolution of FPP in anoles is suggestive of an adaptive process, with selection actively maintaining pattern variants. No studies have identified any selective agents, however, and the presence of FPP in anoles could be random (Calsbeek and Cox, 2012).

A number of explanations could account for pattern variations in animals in general, and in *A. sagrei* in particular. Pattern variants could function in communication, facilitating mating success and species recognition, or play a role in predator avoidance (Calsbeek and Cox, 2012). When male *Anolis* are patterned, the display is typically colorful and may accompa-

ny a reduced dewlap, suggesting a possible function in communication (Losos, 2009). However, Cox and Calsbeek (2011) noted that fixed dorsal patterns in female *A. sagrei* apparently do not function in social communication. They also reported that different pattern morphs do not differ in reproductive rates or strategies, arguing against the hypothesis that patterns function in mate attraction. Furthermore, no observations suggest that patterns are used in either inter- or intrasexual signaling (Cox and Calsbeek, 2011). If FPP in *A. sagrei* is adaptive, it should be associated with some survival advantage and, in fact,

Calsbeek et al. (2008) tested the immunocompetency of the three morph types and found that they differed in immune responses; bar morphs had the strongest response to an injected mitogen and diamond-bar morphs the weakest, with diamond morphs intermediate.

Both among and within species of anoles, attempts to correlate environmental, behavioral, or physiological factors with polymorphism generally have failed (R. Calsbeek, personal communication). Three pattern morphs in female *A. polylepis* were similar in body size and various ecological factors, but differed in perch heights (Steffen, 2010). However, data have yet to show such a correlation in *A. sagrei* (Calsbeek and Cox, 2012).

Within polymorphic species, not all populations exhibit FPP (Paemelaere, 2010). Also, demonstrated correlations vary within polymorphic populations. For example, Calsbeek et al. (2008) found that *A. sagrei* morphs on Great Exuma did not differ in snout-vent length (SVL), but Calsbeek et al. (2010) found differences in SVL among morphs on both Great Exuma and Eleuthera. Furthermore, a relationship between morph type and perch diameter was supported for a population on Great Abaco Island (Schoener and Schoener, 1976), but Calsbeek et al. (2008) found no such relationship in a population near George Town, Great Exuma. At the very least, relationships between morph type and any ecological factor are complicated and might differ over temporal and spatial gradients.

Another possible explanation for the presence of different morphs is that patterns aid in predator avoidance or evasion. Predation is certainly a concern for female Brown Anoles, and speculating that dorsal pattern variation might help them avoid visual predators is not unreasonable (Calsbeek and Cox, 2012). Visual patterns are commonly linked to some form of crypsis (mimicry or camouflage) that reduces predation risk (e.g., Endler, 1980; Brodie, 1993). Paemelaere (2010) suggested that different *Anolis* morphs might select different microhabitats based on their dorsal patterns in order to enhance crypsis and thus minimize predatory recognition. In fact, she determined experimentally that predator at-

tack rates differed between morph models depending on the substrate on which they were positioned (e.g., live leaves vs. thin stems).

In addition to reducing the rate of initial predator recognition, different visual patterns could improve an anole's ability to escape from predators after recognition. In some squamates, color pattern and antipredator behaviors are genetically linked (Brodie, 1989). For example, in the polymorphic Northwestern Gartersnake (*Thamnophis ordinoides*), patterns are correlated with the type of escape behavior and, sometimes, with the extent to which that behavior is performed (Brodie, 1992). Frequency-dependent predation (FDP) predicts that the most common visual morph of a species will suffer the most predation, resulting in changes in morph survival rates over time (Allen and Clarke, 1984; Paemelaere et al., 2011b). Observed survival rates between pattern morphs (which had unequal frequencies) were equal in *Anolis humilis*, which suggests that either FDP does not occur, or it occurs in conjunction with other factors that balance survival rates among morphs (Paemelaere et al., 2011b). Calsbeek et al. (2010) found that the differing survival rates of pattern morphs in *A. sagrei* populations fluctuated over time, however, which is suggestive of frequency-dependent selection on morphs and a possible relationship between pattern type and predation.

In June 2012 on Eleuthera Island, Bahamas, we studied a population of *A. sagrei* to test the hypothesis that female pattern morphs differ in behavioral responses to a putative predator. We asked three questions: (1) Do female morphs differ in habitat use (e.g., Schoener and Schoener, 1976)? (2) Do morph types differ in performance? (3) Do morph types differ in escape behavior? To answer these questions, we collected morphological and associated ecological data for 103 lizards, and recorded escape responses in the field and sprint speeds in the laboratory.

MATERIALS AND METHODS

Collection and observations.—We collected lizards along the edges of ~0.6 km of old cart trails behind the ruins of a clubhouse near



FIG. 2.—The vegetation at the study site near Cape Eleuthera, Bahamas, was characterized by scrub, palm and palmetto stands, and scattered larger hardwoods.

Cape Eleuthera, Eleuthera, Commonwealth of the Bahamas ($24^{\circ}49'–50'N$, $76^{\circ}19'W$; WGS84). The trails were flanked by successional tropical dry forest with some deciduous foliage, resulting in palm and palmetto stands along trail margins with scattered larger hardwoods (e.g., *Bursera simaruba*) with crown heights to 15–20 m (Fig. 2). This is characteristic of legume scrub and human-induced palm–palmetto scrub plant communities (Campbell, 1982).

We walked the trails daily from 3 to 20 June 2012 at 0900 to 1215 h and 1300 to 1400 h. We initially attempted to catch every female *Anolis sagrei* with the goal of catching 30 of each of the three dorsal-pattern morphs, but toward the end of the sampling period, individuals were captured selectively to assure comparably sized samples; consequently, we did not evaluate frequencies of morph types. For each individual, we recorded date, time,

perch height, perch diameter, orientation (i.e., facing up or down or situated horizontally), light (sun, shade, mosaic), morph type, and substrate (branch, trunk, leaf, ground). Perch data applied to where an animal was originally sighted. Unless the original perch was known, data for animals that moved in response to our presence were not included. We also determined, by palpating individual anoles, whether an individual contained a large shelled egg.

Sprint speed.—We determined sprint speed by running animals on a wooden dowel (diameter 2.5 cm), marked with contrasting white tape at 10-cm intervals, and set at an angle of 20° (as per Calsbeek and Irschick, 2007). Runs were conducted at ambient indoor temperature ($\sim 25^{\circ}C$) from 1400 to 1800 h on the day of capture and recorded at 240 frames per second using a high-speed camera (Casio EX-ZR100; Casio Computer Co., Ltd., Tokyo, Japan). Lizards were posi-

tioned at the bottom of the track and persuaded to run with a finger tap. We ran each lizard three times with an hour of rest between runs. If a lizard did not complete at least one full 10-cm sprint, it was rerun. To calculate speed (cm/s), we used ImageJ (National Institutes of Health, Bethesda, Maryland, USA) to count the number of frames during which the lizard moved 10 cm. We selected the fastest speed over any 10-cm span from any of the three trials. Following the three runs, we measured the SVL and hindlimb span of each lizard using a transparent plastic ruler. Hindlimb span was recorded as the distance between the outermost lamellae of the longest toes of both legs while they were manually extended perpendicular to the body. We recorded mass with a digital scale, individually marked each lizard with nontoxic paint, photographed it, and released it at the site of capture.

Escape behavior.—We recorded escape behavior in female *A. sagrei* with different dorsal patterns using procedures modified from Schneider et al. (2000). The same person approached a lizard at a constant pace (~ 0.8 m/s). Once it responded, we used a Leica Disto™ Classic 5 handheld laser distance meter (Leica Geosystems AG, Heerbrugg, Switzerland) to measure the horizontal distance from the observer to the lizard's original perch site. We recorded the lizard's response as running up, running down, running laterally, jumping, and squirreling (a movement around the circumference of the perch that puts the lizard out of view; Greenberg, 1977). Information collected for each individual included date, time, lizard ID, morph type, orientation on the perch, perch height, perch diameter, perch type, light, temperature 1 cm above the perch, and the approach distance and response. To avoid approaching the same individual more than once, we recaptured and remarked animals if paint was fading or if the lizard was shedding. We did include some unmarked lizards in the study. In those instances, we used the same procedure, with morph type being recorded instead of unique identity. When possible, we captured the lizard and determined sprint-speed before marking and releasing it. However, when we were unable to catch an unmarked animal, the

location was flagged and labeled with morph type. To avoid resampling, we made no observations of unmarked animals of the same morph type near a flagged location.

We used the photographs of each individual to confirm morph type before we conducted statistical analyses. We only classified lizards as diamond morphs if the pattern was continuous along the entire length of the dorsum. Our striped category included individuals that had some lateral scalloping of the stripes, as long as this was restricted to the shoulder. Our diamond-bar category included lizards that could not be classified as diamond morphs because pattern edges were vague or the pattern did not extend the full length of the dorsum. This group also included individuals that could not be considered striped because scalloping extended well beyond the shoulder.

Statistical analyses.—We analyzed all data using the statistical program R (v2.15.1; R Core Team, 2012). We \log_{10} -transformed all morphological and sprint speed data prior to analysis and tested for normality. We tested for differences among pattern morphs using analysis of covariance (ANCOVA) with \log -transformed SVL as a covariate. We tested for correlations between lizard body size and approach distance. We did not detect any significant correlations, so we tested for differences in escape behavior among pattern morphs using analysis of variance (ANOVA). For all analyses, we used Tukey–Kramer post-hoc tests to test for pair-wise differences among morphs. We used nonparametric tests (Kruskal–Wallis comparisons and Dunn's pair-wise post-tests) for data sets that were not normally distributed. For all tests, $\alpha = 0.05$.

RESULTS

Sprint speed and perch use.—We collected and tested 29 diamond morphs, 42 diamond-bar morphs, and 32 striped morphs for 103 total individuals. Neither SVL nor mass differed as a function of morph type (Table 1; ANOVA, $P \geq 0.17$). Hindlimb span was correlated with SVL ($F_{1,99} = 68.45$, $P < 0.001$), and differed among morph types as indicated by a statistically significant intercept

TABLE 1.—Sprint speeds, with snout–vent length (SVL) and mass, for each morph type of *Anolis sagrei* collected near Cape Eleuthera, Bahamas (striped morphs = S, diamond morphs = D, diamond–bar morphs = DB). Means are reported ± 1 standard error (SE).

Morph type	Sprint speed (cm/s)		Body size	
	Mean ± 1 SE	Min–max	SVL ± 1 SE (mm)	Mass ± 1 SE (g)
D	81.44 \pm 2.84	55.81–114.29	38.03 \pm 0.38	1.61 \pm 0.05
DB	77.68 \pm 2.62	50.00–109.09	37.57 \pm 0.37	1.64 \pm 0.05
S	74.32 \pm 2.16	42.11–96.00	37.00 \pm 0.33	1.58 \pm 0.05

term ($F_{2,99} = 4.70$, $P = 0.01$, $n = 103$); striped individuals had shorter hindlimb spans than diamond (Tukey Honestly Significant Difference; $P = 0.04$) and diamond–bar morphs ($P = 0.02$).

Overall, SVL was weakly correlated with maximal sprint speed ($r^2 = 0.04$, $P = 0.055$). In addition, maximum sprint speed was similar among pattern variants (ANCOVA; $F_{2,99} = 1.07$, $P = 0.35$). Neither the scaling of hindlimb span with SVL, nor the scaling of sprint speed with SVL, differed among pattern variants; thus, we tested for a correlation between relative hindlimb span and relative sprint speed across all individuals using residuals from linear regressions of each

on SVL. In all, relative sprint speed was weakly correlated with relative hindlimb span ($r^2 = 0.05$, $P = 0.02$; Fig. 3). Thus, regardless of morph type, individuals with relatively broader hindlimb spans tended to sprint relatively faster. Sprint speed was not correlated with perch height or perch diameter ($P \geq 0.17$).

Morph types did not perch on structures of differing diameters (Kruskal–Wallis test; $P = 0.86$). We did find differences among morphs in perch height ($df = 2$, $H = 6.29$, $P = 0.04$, $n = 101$), however, with striped individuals perching higher than diamond ($P = 0.03$) and diamond–bar morphs ($P = 0.03$). Independent of morph type, perch height was positively correlated with lizard mass ($r^2 = 0.09$, $P = 0.002$, $n = 101$), although this relationship was influenced by two relatively heavy individuals that perched exceptionally high. After excluding these two individuals, we no longer recovered a significant relationship ($r^2 = 0.015$, $P = 0.22$, $n = 99$). We also found a weak correlation between perch diameter and lizard mass ($r^2 = 0.05$, $P = 0.049$, $n = 77$).

Escape behavior.—We observed the escape behavior of 44 previously marked individuals with corresponding sprint-speed data, plus 40 additional unmarked lizards for 84 total observations. Morph type did not influence approach distance (ANOVA, $P = 0.086$).

We did not recover a relationship between approach distance and the independent variables of perch height, perch diameter, absolute sprint speed, or relative sprint speed ($P > 0.15$). However, approach distances showed a weak negative correlation with air temperature ($r^2 = 0.052$, $P = 0.03$, $n = 84$). Approach distance differed depending on lizard orientation (ANOVA; $F_{2,81} = 3.17$, $P = 0.047$, $n = 84$), with individuals facing down allowing a

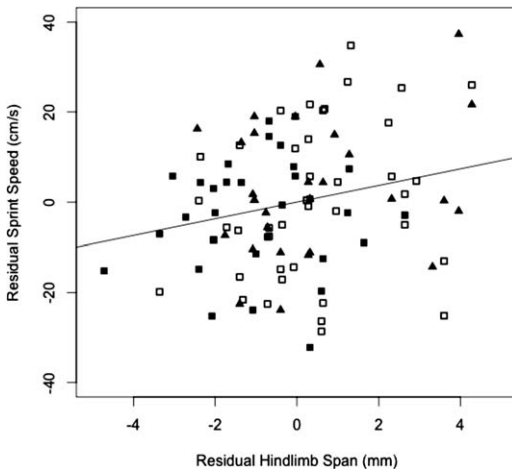


FIG. 3.—The relationship between residual sprint speed and residual hindlimb length for *Anolis sagrei* collected near Cape Eleuthera, Bahamas. Lizards with relatively longer limbs sprinted relatively faster than those with shorter limbs (filled squares = diamond morphs, open squares = diamond–bar morphs, filled triangles = striped morphs).

closer approach before fleeing than those perched horizontally ($P = 0.049$). Destinations to which lizards moved were not related to approach distance (ANOVA; $F_{2,81} = 1.57$, $P = 0.22$, $n = 84$).

DISCUSSION

Sprint speed.—Female *Anolis sagrei* at our site on Cape Eleuthera varied by morph type for some characters. Most obviously, striped morphs had shorter hindlimb spans than both diamond and diamond-bar morphs. Interestingly, hindlimb length is a plastic phenotypic trait in *A. sagrei* (e.g., Losos et al., 2000). Consequently, we do not know whether the difference in hindlimb span within our population is genetic or plastic. If it is a plastic response, then what factor might be responsible for the observed difference? In closed laboratory settings, raising hatchling anoles in settings with broad surfaces produced lizards with longer hindlimbs than those raised in cages with narrower surfaces (Losos et al., 2000, 2001; Kolbe and Losos, 2005). Additional studies should be conducted, however, in order to identify the cause of hindlimb length variation among morphs in natural settings.

Calsbeek et al. (2010) found that *A. sagrei* morphs on the same island differed in SVL. In their study population, diamond morphs were larger than both of the other morph types. Our data indicated that diamond morphs tended toward larger sizes, but only a comparison with striped individuals approached significance. Consequently, we cannot confirm a relationship between morph type and body size, although our data are suggestive of a connection. Also, the presence or absence of such a relationship apparently can differ among populations, even within the same relatively small (in our case, 518-km²) island.

Although Schoener and Schoener (1976) showed a relationship between perch diameter and morph type for *A. sagrei* on Great Abaco Island, our data do not support this pattern on Eleuthera. We did find a relationship between morph type and perch height, however, with striped morphs perching higher than both diamond and diamond-bar morphs.

Previous studies have not shown such a correlation for *A. sagrei* (R. Calsbeek, personal communication); however, Steffen (2010) demonstrated a similar pattern in *A. polylepis* morphs. Females of this species can be grouped into three categories (diamond stripe, checkered stripe, and white stripe) that bear some resemblance to those of female *A. sagrei*. As in our study, Steffen (2010) found that diamond-stripe morphs, like our diamond morphs, perched lowest and white-stripe morphs, like our striped individuals, perched highest. In some environments, perching at different heights might be advantageous for different morphs. Certain combinations of dorsal patterns and environmental conditions at different perch heights could be less visibly conspicuous, possibly reducing predation rates (Steffen, 2010).

We found that mass was positively correlated with perch height and diameter. This trend was not supported, however, once two individuals with extreme values were excluded from the analysis. Among nonoutliers, mass was not a predictor of perch height. The two outliers were the second- and third-heaviest and used the highest perches of any lizards in our sample (perch heights were 4.5× the remaining average). Several previous studies (e.g., Hite et al., 2008) showed positive relationships between anole body size and both perch height and diameter (although those studies included males and females).

Sprint speed in lizards has been shown to correlate with hindlimb length (Losos and Sinervo, 1989; Bonine and Garland, 1999), and our data appear to support this contention. Although the difference was not significant, striped morphs tended to sprint slower than diamond morphs, which likely reflected the shorter hindlimbs of the former.

Escape behavior.—Morph type did not affect any aspect of escape behavior; therefore, we tentatively reject our hypothesis that such behaviors would vary between pattern morphs. Similarly, Calsbeek and Cox (2012) found no difference in the frequencies of fleeing or remaining immobile among pattern morphs in *A. sagrei* facing a putative predator. In North America, however, gartersnakes with a striped pattern usually flee, whereas other morphs tend to remain in place, relying on

camouflage and aggressive behaviors to deter predation (Jackson et al., 1976). Male South African Flat Lizards (*Platysaurus intermedius*), a species that is sexually dichromatic, took refuge earlier than adult females and also fled over shorter distances, indicating that females rely on crypsis as an escape strategy (Lailvaux et al., 2003).

The fact that pattern morphs in *A. sagrei* do not appear to differ in escape responses suggests that escape behavior might not be genetically linked to morph types in this species as it appears to be in some other squamates. Another possibility is that our approaches, although eliciting escape responses, differed from reactions to natural predators (Stuart-Fox et al., 2006). Whereas prey species might respond differently to different types of threats, controlled human approach is a classical experimental surrogate for a natural predator (e.g., Heatwole, 1968; Jackson et al., 1976; Cooper, 1997).

Although our observations of escape behaviors failed to elucidate any mechanism(s) that could maintain FPP, some aspects of observed responses bear further analysis. Females in this population reacted at greater distances during cooler temperatures. Individuals on higher perches generally ran, and most frequently ran down. Vegetation might be less dense around higher perches, making jumping and squirreling less desirable options than running down toward more cover. Lizards perched on trunks and individuals facing down usually squirreled, whereas lizards on branches and those perched horizontally ran. We suspect that lizards used these response patterns because they were most physiologically or energetically convenient.

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