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RESEARCH ARTICLE

Blue-tailed skinks have predation-dependent threat discrimination

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Abstract

The extent to which prey respond to predation risk may depend upon the level of threat it perceives. A prey's perception of a threat can also be influenced by the background levels of predatory threat in the environment. Many animals also rely on visual cues to discriminate threat and assess risk. Eyes, in particular, are known to elicit an aversive response in prey. However, there is a lack of the literature about what salient physical features of a predator's gaze triggers aversion in prey, especially reptilian prey. We capitalized on the putatively aversive effects of eyes to better understand the influence of average background threat on risk perception. We approached blue-tailed skinks (*Emoia impar*) with four different treatments: a blank control and three experimental treatments (two circular eyes, two squares, and one big circle) to test whether eye shape or number induced a greater aversive response in prey measured by the time allocated to key activities, as well as by flight initiation distance (FID) in locations of high and low background threat. Skinks discriminated more between treatments at low risk than in high risk situations by varying their behavior in response to treatments only in low-risk scenarios, but this did not translate into differences in FID. Our results suggest that in high-risk situations, the cost to discriminate is higher than at low risk. Although we can assume our treatments were not perceived as eyes due to a lack of discrimination toward the two circle treatment, detectability and more specifically diameter of stimuli are the most salient to skinks. While skinks are able to detect subtle differences in visual stimuli, this does not affect their overall fear response. Remarkably, skinks, a species not hunted by humans, have the ability to discriminate subtle features about them, a finding that is seen in other species and requires more study.

KEYWORDS
Emoia impar, eyespot discrimination, flight initiation distance, risk assessment, threat perception

1 | INTRODUCTION

Organisms use a variety of different sensory modalities (i.e., visual, olfactory, acoustic, and tactile) to detect cues that provide information that enhances survival (Von der Emde & Warrant, 2015). Specific cues are used to identify food (Krebs & Inman, 1992), mates (Crews & Moore, 1986), and to assess risk, which often involves detecting predators (Apfelbach et al., 2005). Early detection of predators is crucial for fitness, especially for prey that rely on escape. Upon detecting a predator, an individual may flee the area or flee to

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a refuge safe from predators (Blumstein et al., 2016). However, prey not only must escape from predators, but they must also allocate time for other essential activities such as eating and mating, which creates inevitable trade-offs (Cooper Jr & Blumstein, 2015; Lima & Dill, 1990).

To decide when to flee, prey have to weigh the costs of predation risk from staying versus leaving (Cooper Jr & Blumstein, 2015; Lima & Dill, 1990; Ydenberg & Dill, 1986). A decision to flee may be affected by the background level of threat in their environment. For example, guppies (*Poecilia reticulata*) and wood frog tadpoles (*Lythobates sylvaticus*) from high-risk environments responded to novel predators, whereas those from low-risk environments did not (Brown et al., 2013). Similarly, convict cichlids (*Amatitlania nigrofasciata*) responded to a novel predator cue more when pre-exposed to a high-risk environment such that their response matched the level of background of threat (Brown et al., 2014). In riskier environments, predators may elicit a stronger anti-predator response in prey, which may lead to prey escaping sooner.

The cues that an individual detects may influence the specific nature of their response. More specifically, prey may also assess the level of risk from predators by attending to specific visual stimuli. A variety of studies have shown that predator size, speed, and the number of predators modify risk assessment decisions in a variety of species (Cooper Jr & Blumstein, 2015; Lima & Dill, 1990; Møller et al., 2019; Samia et al., 2019; Stankowich & Blumstein, 2005). Eyes and eyespots are also an aversive stimulus to many prey species (Coss, 1979; Curio, 1975; Davidson & Clayton, 2016). Black iguanas (*Ctenosaura similis*) flee sooner when approached by a person with larger artificial eyes as opposed to smaller artificial eyes (Burger et al., 1991). Moreover, the predator's gaze can provide information for escape as prey assess where the predator is actually looking (Davidson et al., 2014). Indian rock lizards (*Psammophilus dorsalis*) had longer FIDs when approached with a direct gaze than when approached with an averted gaze (Sreekar & Quader, 2013). This shows that variation in the type of gaze is associated with variation in prey risk assessment.

It is unclear what specific physical features of predator gaze trigger aversion in prey. Prey may rely on shape (i.e., circles) and the number of stimuli (two eyespots) to recognize a predator's eyes, which triggers its antipredator behavior. Domesticated leghorn chicks (*Gallus domesticus*) did not respond differently to round eyes or square eyes, but the authors stated that more experimentation was needed to better understand the importance of eye circularity in causing aversion (Scaife, 1976a). Additionally, when varying the number of eyes (one or two), chicks responded more aversively to two eyes (Scaife, 1976b), likely because it is visually similar to a predator with binocular vision. Indeed, juvenile African jewel fish (*Hemichromis bimaculatus*), when presented with zero to four eyespots in varying orientations, had the greatest flight activity in response to two eye spots oriented horizontally (Coss, 1979).

It is also possible that the eye color (often black) stands out against the background and captures an individual's attention. A black spot may be conspicuous, and thus elicit increased attention/vigilance as found in previous work that reported that eyespot coloration in prey deters avian predators because of its relative conspicuousness (Stevens et al., 2008). Most prior eyespot studies have not controlled for the total area of the eyespots presented to the prey. Controlling for the total area is essential to understand the mechanisms by which eyespots work to capture an individual's attention because an increase in the spot area, not the number or shape, could have led to aversive responses in prey. This behavior has also been spotted in reptiles. Spitting cobras (*Naja nigricollis* and *N. panida*) have been documented to spray venom either between both human eyes or at one specific human eye, suggesting that they are sensitive to the eye schema of human beings (Westhoff et al., 2005). In anoles (*Anolis carolinensis*), larger pupil size, which affects image salience, can cause reliably longer duration of tonic immobility, a defensive mechanism that can appear when faced with extreme risk (Hennig, 1977).

The ability to discriminate between visual stimuli can also be influenced by background levels of predation threat. Black iguanas from high human exposure areas, often subjected to human predation, can distinguish between direct and tangential approaches, whereas iguanas from no human exposure areas are less able (Burger & Gochfeld, 1990). Guppies experimentally exposed to higher levels of predation risk are better able to discriminate between disturbance cues chemically released by other guppies as a warning of nearby danger (Goldman et al., 2021). Furthermore, damselfish (*Pomacentrus chrysurus*) from a high predation risk environment had a higher intensity antipredator response to predator odor than fish from a low-risk background following conditioning (Chivers et al., 2014).

In light of the above, we studied the importance of background predation risk on eye-spot detection in a skink. We hypothesized that both shape and number of eyespots would be critical for eyespot assessment. Thus, we expected prey would respond most aversively to two circular eyes when compared to square eyes or a single big circle. We also hypothesized that prey from high predation risk environments would discriminate between treatments less when compared to prey from low-risk environments.

We tested these hypotheses on different island populations of blue-tailed skinks (*Emoia impar*) from sites with varying levels of predation risk. We approached them with simulated eyes (two black circles), two black squares, or an area control—a larger circle of equal area, and a no-stimulus control. Standardizing the area of the three experimental treatments was necessary to infer that prey perceived the treatments as eyespots. We evaluated their aversive responses by examining how they changed their time allocated to locomotion and vigilance following experimental presentations and then quantifying their FID as a measure of overall risk assessment. We did this both at "high risk" locations that had relatively more predators and "low risk" locations with relatively fewer predators.

2 | METHODS

2.1 | Study system and experimental procedures

The study was conducted on blue-tailed skinks in Moorea, French Polynesia (17°32′S, 149°50′W). Skinks were studied under University of California Los Angeles (UCLA) IACUC Protocol 2000-147-AR-001 (21 October 2021). Research was conducted under permits issued by the Government of French Polynesia (permit approved on 19 November 2021). Experiments took place between 17 and 27 January 2022 during hours of peak skink activity (08:00–15:30). We conducted experiments in areas of varying levels of human and predatory activity (detailed below). Experimental sites included the Richard B. Gump South Pacific Research Station (17°29′25″S 149°49′35″W), the Te Pu 'Atiti'a cultural center (17°29′34″S 149°49′36″W), the area surrounding the Manutea–Tahiti Rotui Juice Factory and Distillery (17°29′23″S 149°49′43″W), the area surrounding a local soccer field (17°29′18″S 149°49′48″W), an unpaved road in the Opunohu Valley connecting Cook's Bay to Opunohu Bay (17°31′34.3″S 149°50′06.0″W), and an unpaved trail around the perimeter of a pineapple plantation in Opunohu Valley (17°31′21″S 149°49′50″W). We spent 26.86 h at the Gump South Pacific Research Station, 2.02 h at the Te Pu 'Atiti'a cultural center, 4.48 h at the Juice Factory adjacent areas, 5.78 h at the soccer field, 14.6 h at the road in the Opunohu valley, and 21.46 h on the unpaved pineapple plantation trail.

We chose blue-tailed skinks as a study system because of their abundance. Furthermore, skinks have many predators whose abundance varies between locations, creating habitats of differing levels of predation risk. Another study conducted on little brown skinks (*Scinella lateralis*) found they are sensitive to visual cues (Paulissen, 2014), suggesting blue-tailed skinks may also be sensitive to visual cues, which is necessary for our study.

Blue-tailed skinks were abundant at our study sites, so the likelihood of resampling the same individual was very low. We did not resample an area where an individual was flushed in the same day (i.e., a specific pile of litter known to house skinks), and all test subjects were >5 meters (m) away from the previous subject. Blue-tailed skinks are often confused with another species, copper-tailed skinks (*Emoia cyanura*) (Ullrich, n.d.). We distinguished these by tail brightness and body coloration (Zug, 2013). Skinks without a tail were not included in the study since tail loss indicates a recent predator attack which may influence the individual's risk assessment (Cooper Jr & Wilson, 2008). We noted any skinks with partially autotomized tails.

Upon entering a site, to quantify predator activity, we recorded all skink predator sightings during the time we were actively searching for skinks. Skink predators included chickens, cats (*Felis catus*), and mynas (*Acridotheres tristis*). We also recorded dogs (*Canis lupus familiaris*), but we were unclear if they preyed on skinks. Tracking predator activity allowed us to define sites according to predation risk. All trials were conducted when no predators were in sight to limit the chance that skinks would respond to a predator and not the presented stimulus.

For each trial, we recorded the site, wind speed using the Beaufort scale, and the number of conspecifics and heterospecifics of genus *Emoia* within a meter of the focal subject. Experiments were only carried out under weather conditions of no rain and Beaufort ≤2. We estimated skink size to the nearest centimeter (cm) (±10%, based on training where observers estimated sticks of various sizes).

We created hook and loop fastener-mounted black circles or squares that were laminated and affixed to the non-rimmed side of a white baseball cap (Figure S1). Stimuli included two small circles (3 cm radius) that resembled facing eyes (C), two squares (5.32 cm × 5.32 cm) that were spaced the same distance apart as the two circles (S), a big circle (4.24 cm radius) placed in the center of the cap (BC), and a blank control (N). The total area of the two circles, two squares, and the singular big circle were of equal area (56.6 cm^2). The sizes were selected to maximize the area of the black shape while ensuring that it was presented against a high-contrast white background. The big circle served as a control for determining whether skinks responded to any stimulus presented on a white hat with the same area of black material and if the pairing of two objects was important for eye recognition in skinks. The four treatments were presented using a predetermined random order to avoid possible carryover effects, and each skink was only presented with one treatment.

Three observers walked independently through the six sites in search of skinks while wearing the white baseball cap facing forward. Upon locating a subject at an approximate distance of 2–5 m, the observer stopped and rotated their cap such that the backside of the cap with the pre-applied selected treatment faced the skink. After presenting the treatment, we began a 30 second (s) focal animal sample where we quantified skink behavior by quietly dictating behavioral transitions into an iPhone (Apple Inc.). Our ethogram included the following behaviors: bloat (standing motionless and expanding its body), hop (jumping), look (when its body was still and head fixed; scored this behavior each time it looked a different direction), out of sight, run (rapid locomotion away from its position using all four legs), tail wag (moving its tail), and walk (locomotion from its initial position using all four legs). Recordings of behavioral transitions were scored using the event recording software, JWatcher v. 1.0 (Blumstein & Daniel, 2007), that is used to code behavioral transitions and thus quantify time allocation of these focal animal samples.

Following the focal animal samples, we estimated FID to study whether skink risk perception was modified by our treatments. At the same position the focal was conducted at, the observer dropped a flag at their feet to mark the starting distance (SD). They then began walking towards the skink at a constant rate of 0.5 m/s, following methods outlined in McGowan et al. (2014). All observers were trained to walk at a constant rate of 0.5 m/s prior to the experiment. If the skink turned its head after the observer had started walking, the observer would drop a flag to mark the alert distance (AD). If no AD was observed, it was assumed AD was the same as FID, which was the case for many of our observations. Because of this, we used SD, rather than AD in subsequent analyses. Once the skink had fled, the observer stopped walking and dropped a flag at their feet to mark their own position. The observer then dropped another flag at the skink's position at which it initiated flight. We measured FID (using a meter tape to the nearest 0.5 cm) as the distance between the skink position (last) flag and our position upon noting skink flight. SD was then measured by the distance between the starting position flag (first flag) and the skink's position at which it initiated flight (last flag). When applicable, the AD was measured as the distance between the AD flag and the skink's initial position (last flag).

2.2 | Data processing in JWatcher

Using JWatcher v.1.0 (Blumstein & Daniel, 2007) to analyze the focals, we tabulated the number of occurrences of each behavior in the ethogram and calculated the total time the skink was in sight. We grouped the number of runs, walks, and hops as locomotion, and grouped the number of bloat and tail wags as display. We discovered that displays were very rare (observed in 6.5% of the focal observations), and thus, elected to not further analyze them.

2.3 | Statistical analyses

All statistical analyses were conducted in R (version 4.1.2; R Core Team, 2021), using R packages ggResidpanel (Goode & Rey, 2019), emmeans (Lenth et al., 2022), ggplot2 (Wickham, 2016), car (Fox & Weisberg, 2019), and rsq (Zhang, 2021). We set our alpha to 0.05, and report R^2 values as a measure of model fit.

2.3.1 | Predator analysis

From the number of predators recorded during observation and the duration of each observation, we calculated the predator encounter rate (predators/h). After fitting boxplots for the six different sites, we found there was a notable difference in predator abundance between the upper mountainous sites and lower coastal sites. We then combined all the upper sites and lower sites and verified with a t-test that more predators were seen closer to the coastal road than in the mountains. Thus, we classified the lower coastal sites as high risk and the mountainous sites as low risk.

2.3.2 | Focal & FID analyses

We explored our variables graphically with frequency histograms and box plots. We noted that there appeared to be an observer effect, which was corroborated with an analysis of variance (ANOVA) that tested distance to the subject by observer ($p<.001$) whereby one observer had systematically shorter distances to the subject when they started the experiment. Therefore, subsequent models included the observer as a covariate. We explored the potential for the confounding effects of wind speed, group size, skink size, and partially autotomized skinks by fitting ANOVAs with both focal and FID datasets and found no significant effects for all ($p_{\text{wind speed}}=.313$; $p_{\text{group size}}=.363$; $p_{\text{skink size}}=.794$, $p_{\text{autotomized}}=.805$).

To study whether the number of occurrences of looking and locomotion were explained by treatment, we fitted two Poisson regression models, one for each dependent variable, with an offset reflecting the total amount of time the skink was in view. Our base model was fit with “look” and “locomotion” as the dependent variables, respectively, and the following fixed effects: SD, risk (whether the experiment was conducted at a high- or low-risk site), and observer. Additionally, we added two-way interactions between the treatment and SD, and treatment and risk. While not confounding, we explored the potential obscuring effects of wind speed, group size, skink size, and partial autotomy by sequentially adding them to the model. Wind speed itself ($p_{\text{look}}=.143$; $p_{\text{locomotion}}=.537$) and partial autotomy were not significant ($p_{\text{look}}=.989$; $p_{\text{locomotion}}=.320$). However, group size was significant for both focal models ($p_{\text{look}}<.001$; $p_{\text{locomotion}}=.020$) while skink size was significant for solely the locomotion model ($p_{\text{look}}=.630$; $p_{\text{locomotion}}=.018$). Therefore, we added group size to both models and skink size to the locomotion model as a main effect and as an interaction. We sequentially added the other recorded variables to the model as covariates and found that they were not significant, so none of them were included in the final model. For terms with $p<.1$, we calculated planned comparisons (with no adjustments for multiple comparisons) between treatments using estimated marginal means for significant main effects and using estimated marginal means for linear trends for significant interactions. We planned to compute the Cohen's d effect size for treatment if we detected a significant main effect, but we did not detect a significant main effect.

For the FID analysis, we also explored the variables graphically with frequency histograms and box plots. In addition to the observer effect, we found previously regarding SD that there was an observer effect with an ANOVA ($p<.001$), where one observer had significantly shorter FIDs regardless of their SD. Therefore, we added the variable observer as a covariate. Although there was an observer effect, the results did not change regardless of whether data from that observer were included.

We fitted a linear model to explain variation in skink FID as a function of our treatments. For our FID analysis, our dependent variable was FID, and our fixed effects consisted of treatment, as well as the following covariates: SD, risk, and observer. We also included interactions between the treatments and SD, and treatments and risk. Similarly, we explored the potential obscuring effects of wind speed, group size, skink size, and partial autotomy by sequentially adding them to the model. Wind speed itself, group size, skink size, and partial autotomy were not significant ($p_{\text{wind speed}}=.728$; $p_{\text{group size}}=.541$; $p_{\text{skink size}}=.197$; $p_{\text{autotomized}}=.134$); thus, none of these variables were added to the final model. Additionally, none of the other covariates were significant, and thus, they were not included in the final model. For terms with $p<.1$, we calculated comparisons (with no adjustments for multiple comparisons) between treatments using estimated marginal means for significant main effects and using estimated marginal means for linear trends for significant interactions. There was a significant main effect of treatment; thus, we calculated the Cohen's d effect size for treatment.

We evaluated the assumptions of all models with histograms of the model residuals, the residuals' quantile-quantile plots, and plots of the models' fitted values vs. residuals. Residual analyses were consistent with the assumptions required by the models.

3 | RESULTS

3.1 | Predator analysis

We spent a total of 75.2 h at the different sites searching for skinks and observed a total of 372 predators (159 chickens, 7 cats, 133 mynas, and 73 dogs). Significantly, more predators were seen during our observations at our coastal sites than the mountainous sites (2.1 ± 0.33 predator sightings per hour at up mountainous sites, 10.8 ± 0.59 sightings per hour at coastal sites: $t = 2.305$, df = 25.484, $p = .030$). For these reasons, we chose to classify the mountainous sites as low risk and the coastal sites as high risk. While it was unclear if dogs are skink predators, the results remained qualitatively the same if dogs were included ($p = .008$) or excluded ($p = .030$).

3.2 | Focal & FID analyses

Our final dataset included 150 focals and FID observations starting at an average ± SEM distance of 3.35 ± 0.073 m from the skinks. The range of skink sizes was 4–15 cm with an average size of 9.0 ± 0.18 cm. There was a mean of 4.2 ± 0.29 looks and 1.1 ± 0.18 locomotion occurrences per focal. The mean FID for all trials was 1.9 ± 0.05 m. For both focal and FID trials, 76 observations were conducted in high-risk sites (coastal) and 74 in low-risk sites (mountainous).

The Poisson regression model for looking explained 11% of the variation (Table 1). There were significant effects of the number of conspecifics and heterospecifics ($p < .001$) and observer ($p = .001$). The treatment effect approached statistical significance ($p = .089$) as did the significant interaction between treatment and risk ($p = .053$). In low-risk sites, and compared to the control presentation, skinks significantly decreased the number of times they looked (Figure 1a) when presented with the big circle (BC) treatment ($p = .013$) and the squares (S) treatment ($p = .041$). The other pairwise comparisons were not significantly different from each other.

The Poisson regression model for locomotion explained 12.5% of the variation (Table 1). There were significant effects of observer ($p < .001$), skink size ($p = .009$), and number of conspecifics and heterospecifics ($p = .034$). Both risk ($p = .070$) and SD ($p = .057$) approached statistical significance. Significant interactions were found between treatment and SD ($p = .017$), treatment and risk ($p = .023$), and treatment and size ($p = .008$). In low-risk sites, skinks moved significantly less (Figure 1b) when exposed to the S treatment when compared to the control ($p = .005$), the BC treatment ($p = .007$), and the circles (C) treatment ($p = .039$). As SD increased, the skinks moved significantly more (Figure 1c) when exposed to the BC treatment than with the control ($p = .003$). While intermediate-sized skinks did not respond differently by treatment in locomotion frequency, skinks of the smallest and largest sizes did (Figure 1d) in the BC treatment when compared to the control ($p = .002$), and S treatment ($p = .004$).

TABLE 1 Results from a Poisson regression identifying significant (bold) or marginally significant (italics) factors that influenced the number of times blue-tailed skinks (*Emoia impar*) looked and locomoted in response to an experimental stimulus presentation. The Poisson regression models explained 11% of the variation in look and 12.5% of the variation in locomotion

Variables	LR Chisq	df	p
(a) Look			
Treatment	*6.529*	*3*	*.089*
Starting distance (SD)	2.323	1	.127
Risk	1.249	1	.264
Group size	**13.440**	**1**	**<.001**
Observer	**13.772**	**2**	**.001**
Treatment × SD	5.918	3	.116
Treatment × Risk	*7.701*	*3*	*.053*
Treatment × Group size	5.604	3	.133
(b) Locomotion			
Treatment	5.128	3	.163
Starting distance (SD)	*3.615*	*1*	*.057*
Risk	*3.283*	*1*	*.070*
Group size	**31.726**	**2**	**<.001**
Observer	**4.487**	**1**	**.034**
Skink size	**6.734**	**1**	**.009**
Treatment × SD	**10.140**	**3**	**.017**
Treatment × Risk	**9.500**	**3**	**.023**
Treatment × Group size	2.091	3	.554
Treatment × Skink size	**11.809**	**3**	**.008**

Throughout all focal analyses, pairwise comparisons suggest a similar effect between the C treatment and all other treatments (C vs. N, BC, and S) as in their response was not significantly different; however, when comparing the control to the BC treatment, responses varied significantly most of the time (Table S1).

The linear model significantly ($p < .001$) explained 48% of the variation in FID (Table 2). The residuals of the FID linear model fit the assumptions. There were significant effects of treatment ($p = .046$), SD ($p < .001$), and observer ($p < .001$), but no significant interactions (Table 2). However, none of the pairwise analyses of FID by treatment were significantly different from each other (Figure 2). Nevertheless, some of the Cohen's d-values between treatments were moderate (N, BC: 0.30; N, C: 0.34; BC, S: 0.22; C, S: 0.25) while the rest were smaller (N, S: 0.09; BC, C: 0.04). The moderate effect

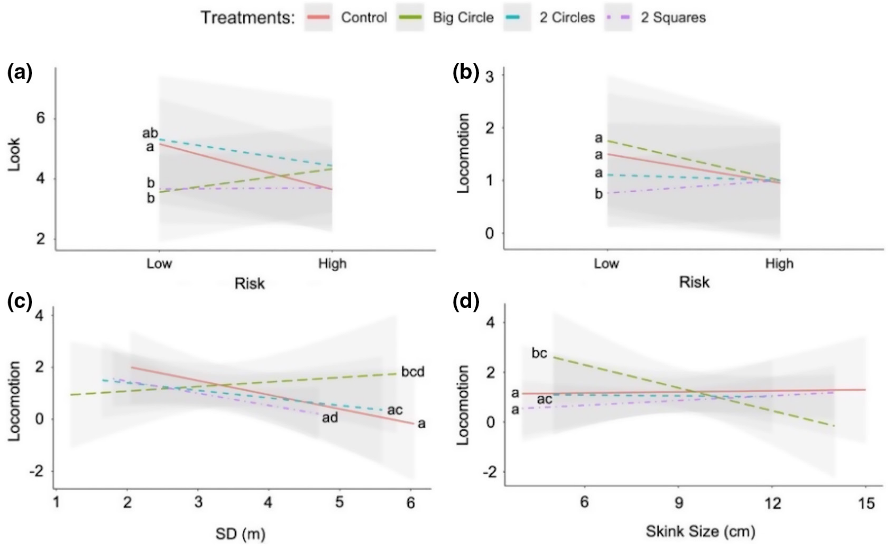

FIGURE 1 Responses—(a) look and (b, c, d) locomotion—of blue-tailed skinks (*Emoia impar*) to experimental approaches, $n = 150$: (a) interaction plot between treatment and risk (high vs. low predation risk) for looking and (b) locomotion; shading represents a 95% confidence interval. Skink behavior varied between treatments at low-risk sites but not high-risk sites. (c) Interaction plot between treatment and starting distance (SD), where skinks discriminated more between treatments at high SD but not low SD. (d) Interaction plot between treatment and skink size where intermediate-sized skinks did not discriminate, but small/large-sized skinks did. The different letters indicate which treatments (lines) are significantly different from each other

TABLE 2 Results from a linear model identifying significant (bold) factors that influenced flight initiation distance (FID) in blue-tailed skinks in response to an experimental stimulus presentation. The model was significant ($p < .001$) and explained 48% of the variation in FID

Variables	df	SS	MS	*F*	*p*
Treatment	**3**	**2.030**	**0.677**	**2.731**	**.046**
Starting distance (SD)	**1**	**21.802**	**21.802**	**87.992**	**<.001**
Risk	1	0.245	0.245	0.990	.321
Observer	**2**	**5.852**	**2.926**	**11.809**	**<.001**
Treatment × SD	3	0.794	0.265	1.069	.365
Treatment × Risk	3	0.308	0.103	0.415	.743
Residuals	136	33.697	0.248		

sizes suggested that upon being approached by a person wearing a white hat with no circles, or a white hat with square eyes, skinks fled earlier than when a person was wearing a white hat with a single large circle or two circular eyes.

4 | DISCUSSION

At the broadest level, our results are consistent with the hypothesis that skinks modify their threat discrimination based on the average background predation risk. They discriminate between threats at low-risk levels but not at high-risk levels. This was detectable in our analyses of looking and locomotion. Skinks in low-risk locations looked more when presented with the control treatment compared to the big circle and squares, but in high-risk locations they did not discriminate between treatments. Analysis of the locomotion data showed that skinks discriminated at low predation risk sites when approached at larger SDs, and as a function of skink size. At high SDs where the observer was further from the skink and thus less of a threat, the skinks were at lower risk and could afford to put energy into discriminating between treatments. This is consistent with previous studies where risk assessment was influenced by the distance at which prey detected a threat (Blumstein, 2003; Blumstein et al., 2004; Fernández-Juricic et al., 2005; Stankowich & Coss, 2006).

Intermediate-sized skinks discriminated between treatments less, and small/large-sized skinks discriminated more as seen in the analysis of their locomotion response. Applying our previous logic would suggest that intermediate-sized skinks are at higher risk and smaller/larger skinks are at lower risk. A possible explanation could be size-based predation affecting risk assessment. For instance, kookaburras (*Dacelo novaeguineae*) preferentially prey on small-medium-sized lizards (Blomberg & Shine, 2000). Such intermediate vulnerability is not always seen, and rough earth snake (*Haldea striatula*) predation risk increases with body size, likely due to higher detection probability by their predators (Taylor & Cox, 2019). In our study, the smallest skinks may be less detectable and thus less exposed to risk while the largest skinks may not be favored by potential

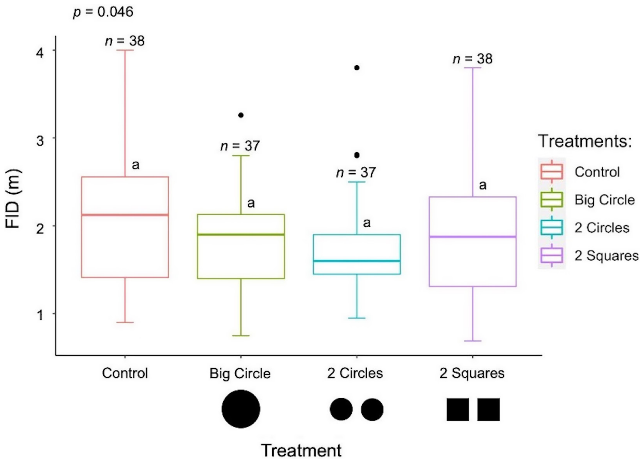

FIGURE 2 Boxplot of flight initiation distance (FID) by treatment. The central line corresponds to the median, the hinges correspond to the first and third quartile, and the whiskers are calculated by 1.5 × interquartile range. Data beyond the whiskers (i.e., outlying points) are plotted individually. When approached by any of the four treatments, blue-tailed skinks did not respond in different ways as illustrated by the pairwise comparisons having the same letter “a” above them

skink predators. If so, this would place intermediate-sized skinks at the highest risk of predation.

Decisions animals make often reflect tradeoffs in costs and benefits. Thus, we infer that for skinks in high-risk situations (high skink predation risk locations, shorter SDs, and intermediate skink sizes) the costs were too high to favor discrimination. Discrimination requires cognitive effort and deprives an individual of energy, attention, and time for other activities essential for survival (Pollard, 2011). Thus, it is more beneficial to discriminate when costs are low. The cost of discrimination may depend on a species' sensory or cognitive ability and the environment. In species with low sensory abilities and those in environments where stimuli detection is difficult or predation pressure is high, discrimination is more costly (Pollard, 2011). In other words, when situations are too risky, it is favorable for prey not to discriminate. Prey commonly demonstrate antipredator flexibility, where their antipredator behaviors are sensitive to the current level of predation risk (Lima & Dill, 1990). Interestingly, this was seen in how skinks allocated time for looking and locomotion, but not in FID.

There were no differences in FID as a function of treatment. Thus, while skinks were able to discriminate among people wearing white hats with different symbols on them, this did not affect their subsequent decision to flee. This result was consistent with Kelligrew et al. (2021) where blue-tailed skinks did not alter FID when exposed to white noise but did increase looking and locomotion rates. Common mynas also adjusted their vigilance behavior after hearing motorcycle sounds compared to silence, but this ultimately did not affect their FID response (Hubbard et al., 2015).

Other studies have shown threat discrimination as a function of predation risk. In Williams et al. (2020), Moorean populations of blue-tailed skinks had more variable antipredator responses in sites that had low human and predator presence but only when FID was quantified, not in time allocated to looking and locomotion. Our results are also consistent with studies conducted on other animals. We note that our quantification of risk is slightly different from those studies where human-populated sites had lower predator abundance (Carrasco & Blumstein, 2012; Coleman et al., 2008; Nickel et al., 2020; Wang et al., 2015), whereas in our study, predator abundance was higher in sites of higher human disturbance (Kelligrew et al., 2021; McGowan et al., 2014; Williams et al., 2020). Regardless, our variable of interest is predator risk, and our observed patterns of predation-based discrimination are consistent with past studies. Mule deer (*Odocoileus hemionus*) showed greater discrimination between alarm calls and non-alarm calls closer to human areas where they are far away from their natural predators (Carrasco & Blumstein, 2012; Waser et al., 2014). Dik-diks (*Madoqua guentheri*) from areas with lower predator abundance (Havmøller et al., 2019; Tinley, 1969) better discriminated between a predator sound and a non-threatening bird song than their conspecifics from areas with higher predator abundance (Coleman et al., 2008). Our study further reinforces the finding that animals discriminate more in environments with lower predator risk. Further research studying the differences in animal response between areas where human disturbance and predator risk are positively associated and areas where human disturbance and predator risk are inversely related could be interesting.

In our study, this pattern of predation-based discrimination was only reflected in the frequency of looking and locomotion and did not influence the skinks' decision to flee. This contrasts with previous studies that found FID to be influenced by predator risk. AD and FID response in mule deer decreased the closer they were to the station, where predators are lower (Price et al., 2014). Additionally, in yellow-bellied marmots (*Marmota flaviventer*), vigilance increased and FID decreased in areas of low predator abundance and high human disturbance (Li et al., 2011). Avian studies have also shown urban birds that face less predation are more tolerant and less wary than their rural counterparts (Cooke, 1980; Donaldson et al., 2007; Evans et al., 2010; Kitchen et al., 2011; Lowry et al., 2011, 2013; Møller, 2008, 2009; Traut & Hostetler, 2003). Although we found no response in FID, skinks perceived the stimuli differently as a function of risk.

While some previous studies of discrimination under different levels of background predation found greater discrimination at higher risk levels, these studies used stimuli that were related to predators of the respective study species (Burger & Gochfeld, 1990; Goldman et al., 2021). In the Burger and Gochfeld (1990) study, walking humans were the experimental treatment for black iguanas in a region where they were hunted by humans. In the Goldman et al. (2021) study, guppies discriminated between alarm cues from conspecifics that warned of nearby danger. Similarly, polymorphic frogs (*Discoglossus galganoi*) were approached by plastic snake models to quantify FID (Zamora-Camacho & Aragón, 2022). In contrast, we manipulated features on hats on potentially threatening, but ultimately benign, humans. Thus, it would be interesting to test the response of skinks to real predator cues in this context.

Our results were not consistent with our a priori hypothesis that skinks assessed risk based on shape and number of eyespots. We find this difficult to interpret but note that we included controls for stimulus surface area that are not normally included in eyespot-type experiments (Coss, 1979; Gallup, 1973; Gallup et al., 1971; Scaife, 1976a, 1976b; Stevens et al., 2008).

We have no evidence that skinks responded uniquely to simulated eyespots as we presented them as shapes on a hat on our head. For both looking and locomotion analyses, skinks did not discriminate between the circle treatment and control and did not discriminate between squares and circle treatments (Table S1). This could be because organisms from the family *Scincidae* use scotopic vision with lower visual acuity, explaining the poor distinction between the two treatments (Hall, 2008). Our results were similar to a previous study on captive leghorn chicks that also did not differentiate between round eyes and square eyes (Scaife, 1976a). Skinks also did not discriminate between the circles and the big circle, indicating that they did not discriminate based on eye number. This result was not consistent with Scaife (1976b) who found chicks responded more adversely to two eyes as opposed to a single eye. Similarly, this is not consistent with other studies on juvenile African jewel fish that found the most flight activity in response to two eyes as opposed to one, three, or four eyes (Coss, 1978, 1979).

However, unlike in Burger et al. (1991), we did not enhance/modify existing eyes, but rather, we put different geometric shapes on our foreheads. This may be responsible for the lack of eyespot recognition as seen from the lack of discrimination between our control and the two circles. In humans and other mammals, the superior colliculus is responsible for the detection and response to face-like stimuli, including eye-like patterns (Nguyen et al., 2013, 2014; Reid et al., 2017). The optic tectum is the primary visual center for lizard visual perception which parallels the mammalian superior colliculus (Stein et al., 1976). Therefore, it is possible that skinks have similar feature detectors that are sensitive to eye-like stimuli. For example, anoles when approached with artificial glass eyes and eyes made from construction paper exhibited prolonged tonic immobility (Hennig, 1977). Yet, in our study, we found no evidence of eye detection; thus, our experimental shapes may not have been perceived strictly as eyes.

However, the size and, more specifically, the diameter of the big circle treatment was the most salient to the skinks as evidenced by the typically significant interactive differences between the big circle and control (Table S1). Thus, stimulus diameter mattered. Our results are consistent with Stevens et al. (2008) that argued it is conspicuousness of contrast and size that elicits aversive responses in prey not eyespot mimicry per se. Martin et al. (2012) suggested large, moving objects are more easily detected. Similarly, McGowan et al. (2014) reported that skinks fled at greater distances when approached by three observers rather than one, which implies that large, moving object(s) are more threatening. Although our results showed the number of objects does not matter (the lack of discrimination between the circles and big circle treatments), these results suggest skinks perceive a greater level of threat when presented with a more detectable stimulus. Comparably, anoles prolong tonic immobility when presented with eyes with black pupils of increasing diameter (Hennig, 1977). In Burger et al. (1991), black iguanas reacted earlier and ran away from faces with larger eye rings than those with smaller eye rings. As all treatments were controlled for area, we can conclude that it is not the area of the object but rather the diameter of the big circle that skinks noticed. Nevertheless, while the big circle affected time allocation to looking and locomotion behaviors, skinks did not change their overall response to the threat in terms of FID.

Concerning the STRANGE criteria, we did not know the sex or age of animals, as all subjects were haphazardly selected in the wild. Because we know predation risk assessment can be affected by age, we did note the size of the subjects, which could be a rough proxy for age (Castoe, 2002; Martín et al., 2021). We could not test on subjects that ran away from us before we completed our focal analysis and put on the treatment, thus our results may show a bias towards more risk-tolerant skinks. However, this method did allow us to have a relatively large sample size (n = 150). It is unlikely that there was extensive pseudoreplication. We studied skinks in six different locations, and there were many skinks in each location. However, it is possible that some resampling occurred since skinks were not marked. Another caveat is that our interobserver reliability might be slightly compromised. Trials were conducted by three different observers after training who were not blind to the treatments. Additionally, we tested, found, and included observer effects in all our statistical analyses, and found interactive effects of treatment and risk even when observer effects were accounted for.

Although we may not fully understand why skinks react a particular way to our treatments, it is apparent that skinks attend to features on a human face. Other animals attend to people's features as well. Gunnison's prairie dogs (*Cynomys gunnisoni*) can distinguish differences in humans from their general shape and clothing color and are reported to encode this information into their alarm calls (Slobodchikoff et al., 1991). In the advent of recent events worldwide, humans regularly wear masks due to the COVID-19 pandemic which does alter one's face. Some species respond to people wearing facial masks. Nubian ibex (*Capra nubiana*) increased vigilance when approached by mask-wearing humans (Yosef et al., 2021). Conversely, Eurasian tree sparrows (*Passer montanus*) reduced their fear response as measured by FID in response to people wearing masks (Jiang et al., 2020). While these effects are varied, it is clear that nonhumans may attend to human facial features.

A broader implication of this study is that what we wear has the potential to modify animal behavior in complex ways. Skinks pay attention to the different shapes presented on hats, suggesting that animals notice what we may consider small changes to objects on the head and potentially even designs on clothing. These may be potential consequences to consider in an ecotourism context. However, while skinks did discriminate between treatments, they did not alter their overall fear response of FID. We hesitate to overgeneralize ecotourism as a negative impact on skinks as a whole, especially as the negative effects of anthropogenic activities on wildlife behavior are already notoriously over-reported (Bateman & Fleming, 2017). Nevertheless, our study illustrates that how animals respond to human features or presented stimuli may be sensitive to variation in background levels of predatory threat. Future discrimination studies should account for background threats.

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CONFLICT OF INTEREST

We declare there is no conflict of interest.

DATA AVAILABILITY STATEMENT

https://github.com/alyssakong/skink.

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