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Defensive behaviors and microhabitat use of *Tropidurus catalanensis* (Squamata, Tropiduridae): body sizes and habitat openness / vegetation cover affect prediction of risk and flight distances

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Abstract. We investigated microhabitat use and defensive behaviors of *Tropidurus catalanensis*, adding information to these practically unknown regards. For each individual caught after visual encounter, we recorded snout-vent length, body mass, substrate and body temperatures, distance from vegetation, distance from a shelter, types of shelter, substrates occupied before and after escaping, flight initiation distance (distance between predator and prey when escaping starts), distance fled (distance ran for escaping), and final flight distance (flight initiation distance plus distance fled). Lizards remained motionless after perceiving the presence of the potential predator trying to keep cryptic and less detectable and monitoring the attacker movements. Longer and heavier individuals tended to run longer distances to avoid threats because were most noticeable and easily detected due to the conspicuousness of their body sizes. During the same period, larger lizards, being faster, were capable to run longer distances than smaller ones. The final flight distance tended to increase as the flight initiation distance and the distances fled increased, allowing to achieve adequate margins of safety. Both before and after fleeing, *T. catalanensis* used mainly rocks. Differences in their prediction of risk made lizards stop closer to woody shelters, and further from the sand, running longer distances to escape. Individuals also may have shown longer distance fled on sand because were less camouflaged there than on rocks. Predictions of risk and fear of lizards increased according to body size and distance from safe places covered by vegetation and near shelters due to microhabitat openness, affecting defensive behaviors of immobility and escape.

Key words: body size, body temperature, defensive mechanisms, distance fled, flight initiation distance, microhabitat temperature.

Introduction

To reduce the chances of detection and capture by predators, animals display various mechanisms of defense, including the extremes of immobility and active escape (Stankowich & Blumstein 2005, Cooper & Blumstein 2015). In lizards, some factors affect individual decision in terms of how likely such defensive behaviors are to occur, for example, body size (Burger & Gochfeld 1990, Cooper et al. 2014, Maia-Carneiro & Rocha 2015), body and microhabitat temperatures (body temperatures – Rand 1964, Rocha & Bergallo 1990, Maia-Carneiro & Rocha 2015; microhabitat temperatures – Martín & López 2000, Diego-Rasilla 2003, Samia et al. 2015), and microhabitats characteristics (Capizzi et al. 2007, Cooper & Wilson 2007, López & Martín 2013), including distance from a shelter and vegetation (Ydenberg & Dill 1986, Stankowich & Blumstein 2005, Cooper & Blumstein 2015). In these regards, larger and older lizards are more shy or fearless than smaller and younger ones (Burger & Gochfeld 1990, Cooper et al. 2014, Cooper & Blumstein 2015); also, lizards which are warmer or on warmer microhabitats are more shy or fearless than colder individuals (Rand 1964, Hertz et al. 1982, Rocha & Bergallo 1990, Cooper & Blumstein 2015, Maia-Carneiro & Rocha 2015); and shyness tends to be comparatively greater far from shelters and in open habitats with less vegetation cover (Stankowich & Blumstein 2005, López & Martín 2013, Cooper & Blumstein 2015). Microhabitat structures and temperatures and body sizes of lizards determine the benefits and costs of staying or fleeing, and thus influence the performing or not of defensive behaviors.

Lizards of the genus *Tropidurus* display a set of defensive mechanisms (Machado et al. 2007, Santana et al. 2011, 2014, Nunes et al. 2012, Maia-Carneiro & Rocha 2015, 2017, 2020a, Maia-Carneiro et al. 2020) and use diverse microhabitats (Vitt 1991, Colli et al. 1992, Santana et al. 2011, 2014, Maia-Carneiro et al. 2020, Maia-Carneiro & Rocha 2020b). We address the question of individual variation in the defensive behavior of *Tropidurus catalanensis* (Squamata, Tropiduridae), a species with geographic distribution in Argentina, Paraguay, Uruguay, and Brazil (Kunz & Borges-Martins 2013, Cacciali & Köhler 2018). In the Brazilian territory, the lizards are found in the states of Rio Grande do Sul, Santa Catarina, Paraná, Mato Grosso do Sul, and São Paulo (Kunz & Borges-Martins 2013, Cacciali & Köhler 2018). Although reports exist on some aspects of the defensive behavior (Maia-Carneiro et al. 2020) and microhabitat use of *T. catalanensis* (Kunz & Borges-Martins 2013, Oliveira et al. 2018, Arruda et al. 2019), the overall pool of information is scant. Here, we investigated defensive behaviors and microhabitat use of *T. catalanensis*, particularly asking whether intrinsic and extrinsic factors influence its defensive behavior. We hypothesized that (1) large body sizes due to enhanced chances of detection, (2) low temperatures due to impaired locomotor performance, and (3) long distances from shelters and vegetation cover are factors likely to increase shyness, in this case operationalized as flight initiation distance, distance fled, and their summation (final flight distance), which defines margins of safety.

Materials and Methods

Study area

Field excursions were carried out in an anthropogenically modified environment in the municipality of Osasco (23°32'32.5" S, 46°45'36.8" W), state of São Paulo, southeastern Brazil. The area of searches was composed of three rectangular-shaped fields located nearby each other. Two were located closer to each other and were composed predominantly by compacted sandy soils, surrounded by wooden planks, concrete walls, leaf litter, shrubs, and trees. The farther field had concrete surface, concrete walls, and also leaf litter, shrubs, and trees in the surroundings. The area was located nearby a small fragment of secondary Atlantic forest. We refer to concrete substrates as rock hereafter.

Data collection

Data were collected through visual encounter surveys across the study area. Searches were carried out on 10 January 2018 and 12 March 2018. Environmental conditions were similar in both summer days. We performed slow walks throughout the area searching for available microhabitats trying to localize lizards visually. Every time an individual was spotted, TMC (first author) moved slowly straight towards it at a constant speed, in all cases wearing similar clothing. Flight initiation distance (FID) was considered as the distance from the potential predator to the lizard at the time of flight (Ydenberg & Dill 1986, Cooper & Frederick 2007, Cooper & Blumstein 2015). The distance fled was defined as the distance ran by a lizard in its first bout of continuous movement until its first stop (Bulova 1994, Stone et al. 1994, Cooper 1997, Cooper & Blumstein 2015). We also estimated the margin of safety of each individual as the sum of FID and distances fled and reported this summation as final flight distance (FFD). Although present in the field during data collection, SLS did not perform visual encounter surveys and kept a distance from TMC and from lizards to avoid interference in the defensive behaviors.

We made capture attempts either manually or through the noose technique. For each captured lizard, we recorded its snout-vent length (SVL – caliper with a precision of 0.01 mm), body mass (spring scales with a precision of 0.25 g), body temperature (T_b – measured with an infrared thermometer with a precision of 0.1 °C), substrate temperature on the microhabitat where it was first seen (T_s – infrared thermometer with a precision of 0.1 °C), distance from a shelter (measuring tape with a precision of 0.1 cm), distance from vegetation (measuring tape with a precision of 0.1 cm), types of the nearest shelter (leaf litter, vegetation, and wood) and of substrates occupied when locomotor escape started and stopped (leaf litter, rock, sand, tree, and wood), FID (measuring tape with a precision of 0.1 cm), distance fled (measuring tape with a precision of 0.1 cm), and FFD (measuring tape with a precision of 0.1 cm). The shelters were defined by observing sites to which lizards escaped after the approximation of the observer. There was no pseudo-replication in our sampling.

Statistical procedures

To evaluate if body size affected flight distances, we made simple linear regression analyses to test for the following relationships: SVL × FID; body mass × FID; SVL × distance fled; body mass × distance fled; SVL × FFD; body mass × FFD. To evaluate if body size influenced microhabitat use and predictions of risk, we performed simple linear regression analyses of SVL and body mass with distance from vegetation, and Spearman non-parametric correlations of SVL and body mass with distance from shelter. To evaluate if body and microhabitat temperatures affected flight distances, we performed simple linear regression analyses of T_b and T_s with FID, distance fled, and FFD. To evaluate if body and microhabitat temperatures influenced microhabitat use and fearfulness, we made simple linear regression analyses of T_b and T_s with distance from vegetation, and Spearman non-parametric correlations of T_b and T_s with distance from shelter. To evaluate if the structure of the environment associated with microhabitats used by the lizards influenced predictions of risk, we performed simple linear regression analyses of distance from vegetation with FID, distance fled, and FFD, and Spearman non-parametric correlations of distance from a shelter with FID, distance fled, and FFD. To evaluate if distances fled were affected by the distance of the potential predator when the escape started, we performed simple linear regression analyses between FID and distance fled. To access the relative contributions of the independent variables SVL, body mass, and distance from vegetation for the dependent variable distance fled, we performed a multiple regression analysis. To evaluate if FFD was dependent on FID and distance fled, we made simple linear regression analyses between FID and FFD, and between distance fled and FFD. To evaluate the relative contributions of FID and distance fled to FFD, we made multiple regression analysis.

To evaluate if the lizards used differentially the types of shelter according with SVL, body mass, T_b, T_s, FID, distance fled, and FFD, we performed analyses of variance. To test if SVL, body mass, T_b, T_s, distances from a shelter and vegetation, FID, distance fled, and FFD differed among types of substrate lizards used before and after the run, we made analyses of variance. In the case of significant results, we employed the Tukey post hoc test for pairwise comparisons. These analyses allowed evaluating for associations among body sizes, body and microhabitat temperatures, microhabitat use, and defensive behaviors. As there was only one observation of root as shelter, we excluded that category to perform statistical analyses. Also due to the reduced number of observations, we excluded the categories leaf litter and wood from the analysis of differences among types of substrate used before the run, and leaf litter, tree, and wood from the analysis of differences among types of substrate used after the flight.

We tested the normality of data distribution through one-sample Kolmogorov-Smirnov and Shapiro-Wilk's statistics (Appendices 1, 2, 3, and 4) for choosing parametric or non-parametric statistics. Whenever necessary, variables were transformed into the logarithms to perform parametric analyses. In non-parametric analyses, we used original values not transformed into the logarithm. We opted to employ parametric statistics even if one of the tests for evaluation of normality of data distribution indicated non-normal distributions if supported by calculations of homogeneity of variances.

Results

Most variables did not interact, but we have found effects from morphology and habitat openness/vegetation cover on distance fled. The lizards ran longer distances if they were larger and farther from vegetation and shelters. There were no relationships between SVL and FID ($F_{1, 18}$ = 2.650; R^2 = 0.128; P = 0.121; N = 20), body mass and FID ($F_{1, 18}$ = 2.517; R^2 = 0.123; P = 0.130; N = 20), SVL and FFD ($F_{1, 18}$ = 2.062; R^2 = 0.103; P = 0.168; N = 20), body mass and FFD ($F_{1, 18}$ = 3.093; R^2 = 0.147; P = 0.096; N = 20), SVL and distance from vegetation ($F_{1, 23}$ = 3.281; R^2 = 0.125; P = 0.083; N = 25), body mass and distance from vegetation ($F_{1, 22}$ = 2.437; R^2 = 0.100; P = 0.133; N = 24), T_b and FID ($F_{1,18}$ = 1.887; R^2 = 0.095; P = 0.186; N = 20), T_b and distance fled ($F_{1, 18}$ = 0.203; R^2 = 0.011; P = 0.658; N = 20), T_b and FFD ($F_{1, 18}$ = 0.418; R^2 = 0.023; P = 0.526; N = 20), T_b and distance from vegetation ($F_{1, 23}$ = 0.264; R^2 = 0.011; P = 0.612, N = 25), T_s and FID ($F_{1, 18}$ = 0.152; R^2 = 0.267; P = 0.702; N = 20), T_s and distance fled ($F_{1, 18}$ = 0.887; R^2 = 0.047; P = 0.359; N = 20), T_s and FFD ($F_{1, 18}$ = 0.161; R^2 = 0.009; P = 0.693; N = 20), T_s and distance from vegetation (F = $_{1, 23}$ = 0.582; R^2 = 0.025; P = 0.453; N = 25), distance from vegetation and FID ($F_{1, 16}$ = 0.100; R^2 = 0.006; P = 0.755; N = 18), distance from vegetation and FFD ($F_{1, 16}$ = 1.667; R^2 = 0.094; P = 0.215; N = 18), and FID and distance fled ($F_{1, 18}$ = 3.364; R^2 = 0.157; P = 0.083; N = 20) (Table 1). There were no correlations of SVL (r = 0.193; P = 0.325; N = 28), body mass (r = 0.276; P = 0.163; N = 27), T_b (r = 0.137; P = 0.486; N = 28), T_s (r = − 0.029; P = 0.882; N = 28), FID (r = 0.191; P = 0.420; N = 20), distance fled (r = 0.215; P = 0.363; N = 20), and FFD (r = 0.299; P = 0.200; N = 20) with distance from shelter (Table

1). Longer ($F_{1, 18}$ = 13.467; R^2 = 0.428; P = 0.002; N = 20; Fig. 1a) and heavier lizards ($F_{1, 18}$ = 13.675; R^2 = 0.432; P = 0.002; N = 20; Fig. 1b) fled longer distances (Table 1). Individuals farther from vegetation also fled for longer distances ($F_{1, 16}$ = 5.790; R^2 = 0.266; P = 0.029; N = 18; Fig. 2; Table 1). A multiple regression analysis ($F_{3, 14}$ = 5.648; R^2 = 0.548; P = 0.009; N = 18) revealed that contrarily to SVL (P = 0.404) and body mass (P =0.087), the distance from vegetation (P=0.009) explained additional portions of the variation of distance fled (Table 1). FFD increased as both FID ($F_{1, 18}$ = 50.554; R^2 = 0.737; P < 0.0001; N = 20; Fig. 3a) and distance fled increased ($F_{1, 18}$ = 10.881; R^2 = 0.377; P = 0.004; N = 20; Fig. 3b) (Table 1). FID (P < 0.0001) and distance fled (P = 0.009) shaped together the FFD ($F_{2, 17}$ = 40.328; R^2 = 0.826; P < 0.0001; N = 20; Fig. 3).

Table 1. Number of observations, arithmetic mean ± one standard deviation (SD), and range of snout-vent length (mm), body mass (g), body and substrate temperatures (°C), distances from vegetation and distance from a shelter (cm), flight initiation distance (cm), distance fled (cm), and final flight distance (cm) of *Tropidurus catalanensis*.

Variable	N	Mean ± SD	Range
Snout-vent length	28	77.57 ± 16.85	31.43 – 98.14
Body mass	27	14.68 ± 7.24	0.75 – 26.75
Body temperature	28	34.37 ± 2.19	29.30 – 39.90
Substrate temperature	28	30.20 ± 4.03	23.50 – 38.90
Distance from vegetation	28	167.88 ± 280.12	0 – 1185.30
Distance from shelter	28	78.18 ± 152.24	0 – 735.00
Flight initiation distance	20	279.63 ± 176.59	60.00 – 781.50
Distance fled	20	96.59 ± 97.705	2.00 – 331.80
Final flight distance	20	376.22 ± 202.05	62.00 – 836.50

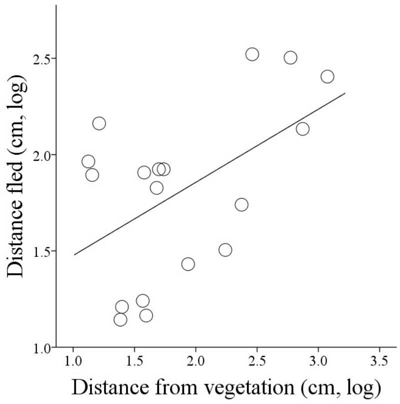
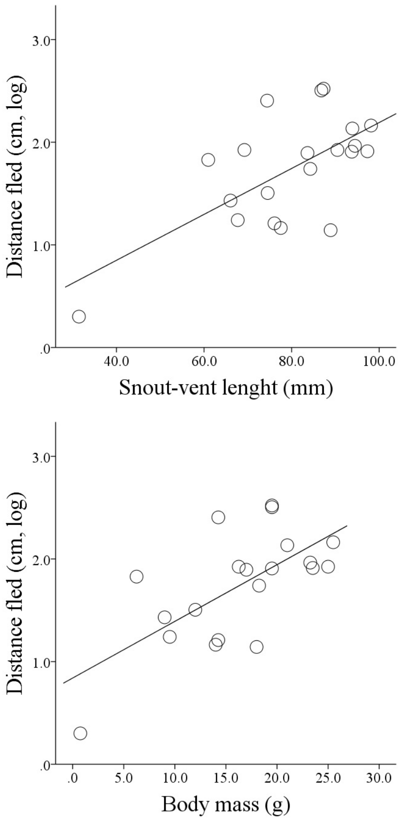


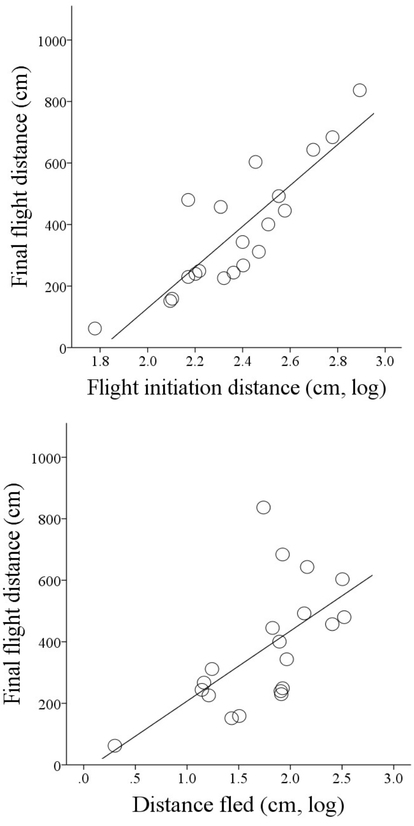
Figure 2. Relationship between distance from vegetation (log-transformed; cm in original scale) and distance fled (in cm) of *Tropidurus catalanensis* in the municipality of Osasco, state of São Paulo, southeastern Brazil. Units of original scale presented for log-transformed data.



a.

b.

Figure 1. Relationships between (a) snout-vent length (in mm) and distance fled (log-transformed; cm in original scale) and between (b) body mass (in g) and distance fled (in cm) of *Tropidurus catalanensis* in the municipality of Osasco, state of São Paulo, southeastern Brazil. Units of original scale presented for log-transformed data.



a.

b.

Figure 3. Relationships between (a) flight initiation distance (log-transformed; cm in original scale) and final flight distance (cm) and between (b) distance fled (log-transformed; cm in original scale) and final flight distance (cm) of *Tropidurus catalanensis* in the municipality of Osasco, state of São Paulo, southeastern Brazil. Units of original scale presented for log-transformed data.

There were no differences among types of shelter regarding SVL ($F_{2, 24}$ = 1.712; R^2 = 0.125; P = 0.202), body mass ($F_{2, 23}$ = 1.832; R^2 = 0.137; P = 0.183), T_b ($F_{2, 24}$ = 0.711; R^2 = 0.056; P = 0.501), T_s ($F_{2, 24}$ = 0.763; R^2 = 0.060; P = 0.477), FID ($F_{2, 16}$ = 0.100; R^2 = 0.012; P = 0.905) (Table 2), and FFD ($F_{2, 16}$ = 1.070; R^2 = 0.118; P = 0.366), but there were with respect to distance fled ($F_{2, 16}$ = 22.769; R^2 = 0.740; P < 0.0001; Fig. 4; Table 2). Pairwise comparisons through Tukey post hoc test indicated similarity between leaf litter and vegetation (P = 0.821), but lizards fled longer distances when the closest shelters were wood than leaf litter (P < 0.0001) and vegetation (P < 0.0001) (Fig. 4; Table 2). Individuals used mainly rock as substrate both before and after running (Table 3). There were no differences of SVL ($F_{1, 24}$ = 1.657; R^2 = 0.065; P = 0.210), body mass ($F_{1, 23}$ = 3.387; R^2 = 0.128; P = 0.079), T_b ($F_{1, 24}$ = 0.126; R^2 = 0.005; P = 0.726), T_s ($F_{1, 24}$ = 0.002; R^2 = 0.000; P = 0.961), FID ($F_{1, 16}$ = 0.249; R^2 = 0.015; P = 0.624), and FFD ($F_{1, 16}$ = 2.658; R^2 = 0.142; P = 0.123) between types of substrate used before to run (Table 4); however, distances from shelter ($F_{1, 23}$ = 19.945; R^2 = 0.464; P < 0.0001; Fig. 5a), from vegetation ($F_{1, 22}$ = 36.905; R^2 = 0.627; P < 0.0001; Fig. 5b), and fled ($F_{1, 16}$ = 44.968; R^2 = 0.738; P < 0.0001; Fig. 5c) were longer on sand than on rock (Fig. 5; Table 4). There were no differences of SVL ($F_{1, 13}$ = 1.794; R^2 = 0.121; P = 0.203), body mass ($F_{1, 13}$ = 1.150; R^2 = 0.081; P = 0.303), T_b ($F_{1, 13}$ = 0.798; R^2 = 0.058; P = 0.388), T_s ($F_{1, 13}$ = 0.036; R^2 = 0.003; P = 0.852), FID ($F_{1, 13}$ = 0.074; R^2 = 0.006; P = 0.790), and FFD ($F_{1, 13}$ = 2.650; R^2 = 0.169; P = 0.128) between types of substrate lizards occupied after flight (Table 5); however, distances from shelter ($F_{1, 13}$ = 50.947; R^2 = 0.797; P < 0.0001; Fig. 6a), from vegetation ($F_{1, 12}$ = 25.126; R^2 = 0.677; P < 0.0001; Fig. 6b), and fled ($F_{1, 13}$ = 13.257; R^2 = 0.505; P = 0.003; Fig. 6c) were longer on sand than on rock substrates (Fig. 5; Table 5).

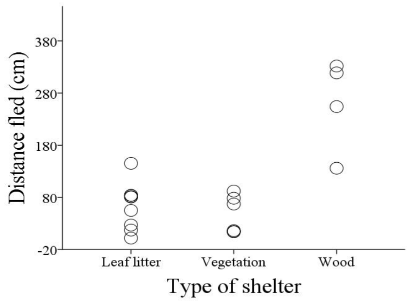


Figure 4. Differences of distance fled (in cm) between types of shelter of *Tropidurus catalanensis* in the municipality of Osasco, state of São Paulo, southeastern Brazil.

Discussion

Tropidurus catalanensis remained motionless after perceiving the presence of the potential predator, apparently trying to keep cryptic and less detectable and monitoring the attacker movements, and ran with increasing risks due to the approaching menace. Keeping immobile allows to conceal the presence and difficult the location by predators and was expected according to observations and predictions (Ydenberg & Dill 1986, Cooper & Frederick 2007, Cooper & Blumstein 2015). Lizards of other *Tropidurus* species also stood still facing potential predators; for example, *T. montanus* in the state of Minas Gerais of Southeastern Brazil (Machado et al. 2007) and *T. hispidus* and *T. semitaeniatus* in the state of Bahia of northeastern Brazil (Maia-Carneiro & Rocha 2015) relied on immobility and crypsis to avoid detection.

Table 2. Number of observations, arithmetic mean ± one standard deviation (SD), and range of flight initiation distance (cm), distance fled (cm), and final flight distance (cm) as distinguished by types of shelter (leaf litter, vegetation, and wood) of *Tropidurus catalanensis*.

Variable	Leaf litter			Vegetation			Wood		
	N	Mean ± SD	Range	N	Mean ± SD	Range	N	Mean ± SD	Range
Snout-vent length	12	74.83 ± 21.03	31.43 – 98.14	9	74.08 ± 13.70	52.48 – 94.47	6	88.80 ± 8.19	74.41 – 97.83
Body mass	12	13.88 ± 8.59	0.750 – 25.50	9	12.97 ± 5.88	5.75 – 23.25	5	20.20 ± 4.47	14.25 –26.75
Body temperature	12	34.53 ± 1.19	32.50 – 36.80	9	33.53 ± 2.19	29.3 – 36.10	6	34.40 ± 2.78	29.60 – 37.20
Substrate temperature	12	30.19 ± 4.12	23.50 – 34.50	9	28.70 ± 3.26	25.00 – 34.20	6	31.02 ± 3.64	27.60 – 37.50
Flight initiation distance	9	314.44 ± 252.18	60.00 – 781.50	6	273.88 ± 63.55	209.60 – 378.00	4	248.13 ± 91.46	148.20 – 356.50
Distance fled	9	64.1 ± 43.96	2.00 – 145.30	6	47.07 ± 36.12	13.90 – 92.10	4	260.13 ± 89.51	135.90 – 331.80
Final flight distance	9	378.54 ± 270.99	62.00 – 836.50	6	320.93 ± 89.58	225.80 – 445.20	4	508.25 ± 65.09	457.20 – 603.40

Table 3. Number of observations (N) and the respective percentages (N%) of substrates used by *Tropidurus catalanensis* before (rock, leaf litter, sand, and wood) and after (rock, leaf litter, sand, tree, and wood) flight.

Substrate	Substrate used before flight		Substrate used after flight	
	N	N%	N	N%
Rock	21	75.00	12	63.16
Leaf litter	1	3.57	1	5.26
Sand	5	17.86	3	15.79
Tree	–	–	2	10.53
Wood	1	3.57	1	5.26
Total	28	100.00	19	100.00

Table 4. Number of observations, arithmetic mean ± one standard deviation (SD), and range of flight initiation distance (cm), distance fled (cm), and final flight distance (cm) as distinguished by types of substrates *Tropidurus catalanensis* used before locomotor escape (rock and sand).

Variable	Rock			Sand		
	N	Mean ± SD	Range	N	Mean ± SD	Range
Snout-vent length	21	77.67 ± 15.57	50.87 – 98.14	5	86.99 ± 7.70	74.41 – 93.88
Body mass	20	14.13 ± 6.97	3.50 – 25.50	5	20.20 ± 4.47	14.25 – 26.75
Body temperature	21	34.11 ± 1.72	29.30 – 36.80	5	34.46 ± 3.10	29.60 – 37.20
Substrate temperature	21	29.81 ± 4.11	23.50 – 37.50	5	29.72 ± 1.99	27.60 – 32.50
Distance from shelter	21	30.37 ± 22.18	10.60 – 94.50	5	274.66 ± 300.09	0 – 735.00
Distance from vegetation	21	59.49 ± 97.89	0 – 426.30	5	655.46 ± 340.34	288.40 – 1185.30
Flight initiation distance	14	315.23 ± 190.96	124.50 – 781.50	4	248.13 ± 91.46	148.20 – 356.50
Distance fled	14	61.24 ± 38.98	13.90 – 145.30	4	260.13 ± 89.51	135.90 – 331.80
Final flight distance	14	376.46 ± 205.17	151.50 – 836.50	4	508.25 ± 65.09	457.20 – 603.40

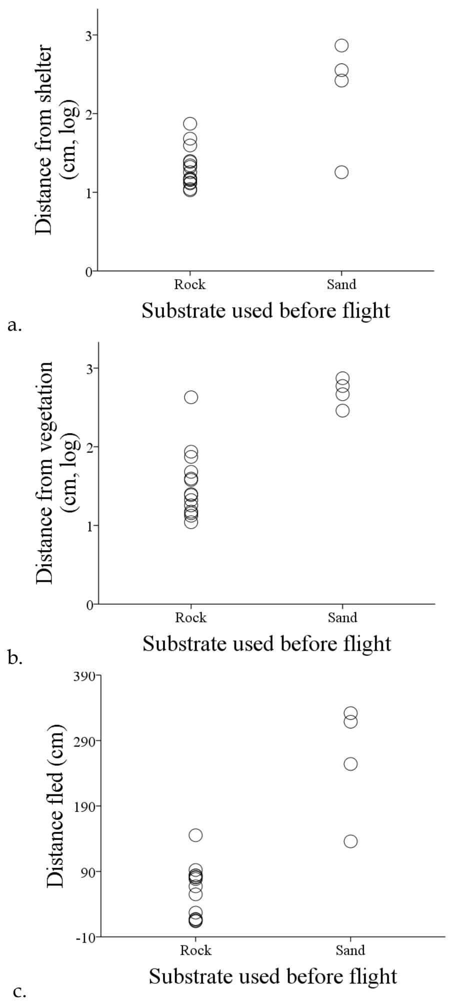


Figure 5. Difference of distances (a) from shelter (log-transformed; cm in original scale), (b) from vegetation (log-transformed; cm in original scale), and (c) fled (in cm) between substrates used before locomotor escape of *Tropidurus catalanensis* in the municipality of Osasco, state of São Paulo, southeastern Brazil. Units of original scale presented for log-transformed data.

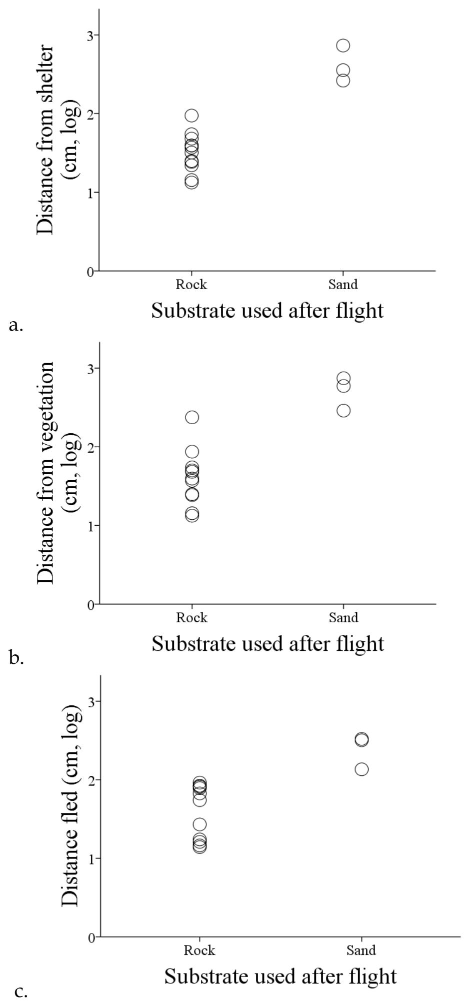


Figure 6. Difference of distances (a) from shelter (log-transformed; cm in original scale), (b) from vegetation (log-transformed; cm in original scale), and (c) fled (log-transformed; cm in original scale) between substrates used after locomotor escape of *Tropidurus catalanensis* in the municipality of Osasco, state of São Paulo, southeastern Brazil. Units of original scale presented for log-transformed data.

Supposedly, visual-oriented predators find prey more easily in open environments like those of *T. montanus* (Machado et al. 2007), *T. hispidus* and *T. semitaeniatus* (Maia-Carneiro & Rocha 2015), and *T. catalanensis* (this study), a condition that makes yet more valuable the ability of remaining undetectable.

Longer and heavier *T. catalanensis* individuals tended to flee longer distances to avoid threats. Larger lizards are more noticeable and easily detected by predators than smaller ones due to the conspicuousness of their body sizes (Bulova 1994, Martín & Pérez 2003, Cooper et al. 2014, Maia-Carneiro & Rocha 2015). Also, larger lizards are capable to run longer distances than smaller ones giving the same time-lapse because they are faster (Huey & Hertz 1982, Losos 1990, Garland & Losos 1994, Stiller & McBrayer 2013). However, distance from vegetation appeared to be a better predictor of distance fled than body size. Similarly, smaller *T. catalanensis* individuals may have fled for shorter distances due to tradeoffs between the trophic, spatial, and/or thermal benefits of staying and the costs of fleeing. For example, it was suggested that small-sized *Lacerta monticola* showed overall shorter flight initiation distances because associated costs of hiding were higher than for large individuals due to their faster cooling rates (Martín & López 2003). Moreover, *Podarcis lilfordi* fled for shorter distances from where they were when food availabilities were greater (Cooper et al. 2006). If lizards diminish distances fled under low probabilities of being caught, they reduce costs associated with fleeing without a substantial increment in predation risk, a decision that depends on their body sizes.

Table 5. Number of observations, arithmetic mean ± one standard deviation (SD), and range of flight initiation distance (cm), distance fled (cm), and final flight distance (cm) as distinguished by types of substrates *Tropidurus catalanensis* used after locomotor escape (rock and sand).

Variable	Rock			Sand		
	N	Mean ± SD	Range	N	Mean ± SD	Range
Snout-vent length	12	79.71 ± 11.96	60.96 – 97.30	3	89.32 ± 3.96	86.78 – 93.88
Body mass	12	16.19 ±5.98	6.25 – 25.00	3	20.00 ± 0.866	19.50 – 21.00
Body temperature	12	33.95 ± 2.17	29.30 – 36.80	3	35.17 ± 1.71	33.20 – 36.30
Substrate temperature	12	29.78 ± 3.62	23.50 – 34.20	3	29.37 ± 1.55	27.60 – 30.50
Distance from shelter	12	36.98 ± 22.12	13.30 – 94.50	3	451.77 ± 249.80	262.90 – 735.00
Distance from vegetation	12	52.45 ± 62.43	0 – 236.80	3	542.00 ± 232.47	288.40 – 745.00
Flight initiation distance	12	313.03 ± 194.52	124.50 – 781.50	3	263.13 ± 105.81	148.20 – 356.50
Distance fled	12	52.61 ± 32.21	13.90 – 92.10	3	262.13 ± 109.52	135.90 – 331.80
Final flight distance	12	365.63 ± 203.60	151.50 – 836.50	3	525.27 ± 67.95	480.00 – 603.40

Lizard microhabitat and body temperatures affect defensive behaviors of locomotor escape (Rand 1964, Cooper & Blumstein 2015, Samia et al. 2015), which did not happen with *T. catalanensis* in our study. Increased wariness is typical of lizards having low body temperatures due to impairment of locomotor capacities, otherwise, those having high body temperatures are often less cautious (Rand 1964, Hertz et al. 1982, Cooper & Blumstein 2015). This is exemplified by Brazilian *T. oreadicus* (Rocha & Bergallo 1990) and *T. hispidus* (Maia-Carneiro & Rocha 2015). Because they may achieve high body temperatures than on colder microhabitats, lizards on warmer sites also could be more fearless (Cooper & Blumstein 2015). Costs and benefits of staying on and fleeing from microhabitats (Martín & López 2003, Cooper et al. 2006, Cooper & Blumstein 2015) also influence the perception of risks.

An escaping prey has to flight distances that allow better avoidance of predation (Cooper 1997; Cooper & Blumstein 2015). Lizards that flee at longer distances from predators would flight shorter distances to escape, whereas individuals that run at shorter distances from attackers would escape for longer distances to be equally safe (Cooper 1997), but distances fled by *T. catalanensis* were not influenced by the distance of the potential predator when they started to escape. However, *T. catalanensis* tended to show longer distances fled when farther from vegetation to achieve safer covered sites (see Fig. 2). Perhaps because the investigator stopped following the lizards after they started to escape (see Cooper 1997), individuals did not necessarily run to refuges, which may explain the lack of associations of flight distances with distance from shelters and of FID with distance fled. Nevertheless, the FFD of *T. catalanensis* tended to increase as the FID and the distance fled increased. Similarly, distances fled by *Plestiodon laticeps* lizards were influenced by distances and directions to refuges and flight initiation distances (Cooper 1997), which jointly allowed to evaluate and to create appropriated margins of safety.

Differences in the prediction of risk made *T. catalanensis* move farther from vegetation, closer to wood shelters, and on the sand, and run longer distances to escape. Moving away from the vegetation the area was sandy and more open, and woody shelters were located closer to open areas than the other types of shelter. Thus, microhabitats with sand substrates were widely open and farther from shelters and vegetation. The few vegetation elements made individuals more conspicuous and susceptible to detection, affecting prediction of risks as reflected in defensive behaviors (Burger & Gochfeld 1993; Bulova 1994; Cooper 1997; Martín & López 1995, 2000). To enhance the chances of escaping, *T. catalanensis* fled longer distances, as expected from lizards in habitats where they face high predation pressures (Stone et al. 1994; Cooper et al. 2009). Lizards of other species (Bulova 1994; Cooper 1997; Martín & López 1995, 2000; López & Martín 2013) also had greater wariness and longer distances fled in places with few covers far from vegetation. Distances fled by *T. catalanensis* when farther from vegetation tended to be longer than nearby vegetation, independently of body size. Also, individuals of this species may have shown longer distance fled on sand because were less camouflaged there than on rocks. Anyhow, demonstrations of distances fled of lizards rely on an assessment of risks with consideration of time and/or space required to get to a safe place.

Both before and after fleeing, *T. catalanensis* used mainly rocks as substrates (microhabitats). Lizards of the genus *Tropidurus* use different kinds of substrates, including bare ground, bromeliads, cacti, fallen wood, leaf litter, fallen tree limbs, sand, shrubs, termite mounds, trees, wall, and rocks, among others, but some species may be found predominantly on rocks (Vitt 1991, Faria & Araújo 2004, Van Sluys et al. 2004, Machado et al. 2007, Meira et al. 2007, Santana et al. 2011, 2014, Gomes et al. 2015). Among other reasons, appropriate microhabitat use has relevance for lizards due to associations with defensive behaviors (Cooper & Wilson 2007, 2000, Attum et al. 2007, Capizzi et al. 2007). Within the genus *Tropidurus*, *T. spinulosus* was found perching at higher heights on tall trees and typically fled climbing upward, whereas *T. oreadicus* occupied lower heights on small trees and ran mainly downward (Colli et al. 1992). The associations of microhabitats used by *T. catalanensis* with distances from a shelter, from vegetation, and distances fled, suggested that, as for other lizard species, the performing of defensive displays was associated with space use (Colli et al. 1992, Attum et al. 2007, Capizzi et al. 2007), including distances from refuges and covered sites (Burger & Gochfeld 1993, Bulova 1994, Cooper 1997, Martín & López 1995, 2000, 2003, Stankowich & Blumstein 2005).

Tropidurus catalanensis ran towards rocks, leaf litter, trees, and wood, but mainly in the direction of rocks. Microhabitats used after escaping vary among lizard species and depend on the specific characteristics of local environments. For example, *Callisaurus draconoides* often escaped towards open microhabitats in open environments and frequently towards vegetation in covered habitats (Bulova 1994). In the genus *Tropidurus*, *T. oreadicus* was common in open areas and frequently used shelters on the ground under and inside logs and termite nests, whereas *T. spinulosus* occurred in sites with dense vegetation, tall trees, and in open areas on rock outcrops and fled only to burrows found in vegetation (Colli et al. 1992). As also observed in other species of *Tropidurus* (Machado et al. 2007, Santana et al. 2011, 2014, Gomes et al. 2015), except for two *T. catalanensis* found on rocks that ran to trees, all the observed individuals fled to the same substrate used before the flight.

The flight initiation distance of *T. catalanensis* averaged 279.63 ± 176.59 cm (ranging from 60.00 cm to 781.50 cm; N = 20); reports of this defensive behavior in Brazilian congeners presented means of 360 cm (170 − 830 cm) for *T. oreadicus* (Rocha & Bergallo 1990) and of 160.5 ± 69.2 (72.8 – 282.0; N = 18) for *T. hispidus* and 92.6 ± 47.0 (22.7 – 196.7; N = 25) for *T. semitaeniatus* (Maia-Carneiro & Rocha 2015). Therefore, *T. catalanensis* seemed less cautious than *T. oreadicus* (Rocha & Bergallo 1990) and more fearful than *T. hispidus* and *T. semitaeniatus* (Maia-Carneiro & Rocha 2015). These differences may have occurred due to differences between environments − although all habitats were predominantly open, that of *T. hispidus* and *T. semitaeniatus* (Igatu) was a more undisturbed, natural, and isolated landscape than the present study area of *T. catalanensis*, which had an environment more modified anthropogenically where the access of humans may stimulate the flight.

Although diverse studies approached aspects of defensive behaviors of lizards, information on this regard is still scarce or nonexistent for most species. This report adds knowledge concerning defensive mechanisms displayed by these animals showing they have different perceptions of risks and escape decisions depending on the body sizes and on the structure of microhabitats, which potentially allow optimizing the success of flight and increasing survivorship. Decisions to escape vary according to costs of staying or fleeing − flight distances may lengthen with increased risks of capture and shorten with increased costs of fleeing. Predictions of risk and wariness of lizards increase according to body sizes and distances from safe places covered by vegetation and near shelters due to microhabitat openness, affecting defensive behaviors of immobility and escape.

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