

Phyllomedusa 18(2):185–193, 2019

© 2019 Universidade de São Paulo - ESALQ

ISSN 1519-1397 (print) / ISSN 2316-9079 (online)

doi: <http://dx.doi.org/10.11606/issn.2316-9079.v18i2p185-193>

Delayed escape responses of male *Basiliscus plumifrons* (Squamata: Corytophanidae) during peak activity

Matthew S. Lattanzio

Department of Organismal and Environmental Biology, Christopher Newport University, Newport News, Virginia 23606, USA. E-mail: matthew.lattanzio@cnu.edu.

Abstract

Delayed escape responses of male *Basiliscus plumifrons* (Squamata: Corytophanidae) during peak activity. Many animals must balance their time spent active in a habitat against their perceived risk of predation. Factors that may increase that perceived risk, such as a faster predator approach, are therefore expected to cause prey to initiate escape quickly to avoid capture. At the same time, because patterns of daily activity can fluctuate throughout the day, the relative costs and benefits of initiating escape may also differ over time. Here I evaluated the escape responses of adult male emerald basilisk (*Basiliscus plumifrons*) lizards in two different time periods: morning (when daily activity peaks) and early afternoon (when activity is suppressed). Further, I approached each lizard at either a practiced slow or fast pace. Escape responses were recorded as flight-initiation (distance between observer and lizard prior to escape) and flight (distance travelled during escape) distance. No factor affected flight distance, and approach speed also had no effect on flight initiation distance. In contrast, time period affected flight initiation distance, with males approached in the morning delaying their escape response compared to males approached during the early afternoon. Because morning and early afternoon periods coincide with peak and suppressed periods of activity for basilisks at this study site, respectively, ambush-foraging species like *B. plumifrons* may delay escape when active to avoid prematurely alerting the predator of their presence.

Keywords: activity, Emerald Basilisk, flight distance, flight-initiation distance, lizard, optimal escape theory.

Resumo

Respostas de fuga atrasadas de machos de *Basiliscus plumifrons* (Squamata: Corytophanidae) durante o pico de atividade. Muitos animais devem equilibrar o tempo gasto em atividade em um habitat com o risco de predação percebido. Portanto, espera-se que fatores que possam aumentar aquele risco, como uma aproximação mais rápida do predador, façam com que a presa inicie a fuga

Received 04 January 2019

Accepted 12 August 2019

Distributed December 2019

rapidamente para evitar a captura. Ao mesmo tempo, como os padrões de atividade diária podem variar ao longo do dia, os custos e benefícios relativos de iniciar a fuga também podem diferir ao longo do tempo. Avaliei aqui as respostas de fuga de machos adultos do basilisco-esmeralda (*Basiliscus plumifrons*) em dois períodos diferentes: manhã (quando a atividade diária atinge o pico) e início da tarde (quando a atividade cessa). Além disso, eu me aproximei de cada lagarto a passos lentos ou rápidos. As respostas de fuga foram registradas como distância de início de fuga (distância entre o observador e o lagarto antes da fuga) e distância de fuga (distância percorrida durante a fuga). Nenhum fator afetou a distância de fuga e a velocidade de aproximação também não teve efeito sobre a distância de início de fuga. Por outro lado, o período de tempo afetou a distância de início de fuga, com os machos abordados de manhã atrasando sua resposta de fuga em comparação com os machos abordados no início da tarde. Como os períodos da manhã e do início da tarde coincidem, respectivamente, com os períodos de atividade máxima e de cessação da atividade para os basiliscos neste local de estudo, predadores de tocaia como *B. plumifrons* podem atrasar a fuga quando ativos para evitar alertar prematuramente o predador sobre sua presença.

Palavras-chave: atividade, basilisco-esmeralda, distância de fuga, distância de iniciação da fuga, lagarto, teoria da fuga ótima.

Introduction

How a prey organism responds to an approaching predator has clear and immediate fitness consequences (Ydenberg and Dill 1986), and it is therefore unsurprising that these responses are well-studied in many taxa (reviewed by Stankowich and Blumstein 2005). A major component of the anti-predation response in lizards, their escape behavior, is often modeled in an economic fashion because of the cost-benefit trade-offs surrounding the decisions of when and how far to flee an approaching predator (e.g., Ydenberg and Dill 1986, Cooper Jr. and Blumstein 2015). This process can be quantified by estimating two parameters: flight-initiation distance and flight distance (FID and FD respectively). Briefly, FID represents the distance between an approaching predator and the lizard prior to its escape and FD is the distance fled by the lizard during the initial escape response (e.g., Lailvaux *et al.* 2003, Cooper Jr. and Frederick 2007). Empirical studies have revealed strong support for this model across several lizard taxa, supporting its utility for understanding the factors affecting escape decisions by this diverse clade (Cooper Jr. 2003a, Martín 2003, Vanhooydonck *et al.*

2007, Cooper Jr. *et al.* 2009, Lattanzio 2009, 2014, Brock *et al.* 2015, Stelatelli *et al.* 2015).

Many factors affecting variation in FID and FD by lizards have been identified (reviewed by Stankowich and Blumstein 2005, Samia *et al.* 2015). For example, individuals that perceive a greater risk of predation often initiate the escape response earlier (i.e., at a greater FID) and flee further than individuals which perceive lesser risk (Ydenberg and Dill 1986). One relatively underappreciated factor that may affect that perception of risk is their level or type of activity at the time of a predatory encounter (Cooper Jr. and Pérez-Mellado 2004, Cooper Jr. 2009). Specifically, many species vary in their frequency and use of different behaviors throughout the day, and so shunting energy from other behaviors to an antipredator response requires consideration of the potential costs of that energetic trade-off. For example, during periods of foraging, the costs of giving up access to resources (food) may lead an individual lizard to delay its escape response (Cooper Jr. *et al.* 2006). In addition to food resources, temperature variability also contributes to shaping variation in daily activity patterns in lizards (Adolph and Porter 1993) and, unsurprisingly, has been associated with variation in their escape decisions as well (e.g.,

Rocha and Bergallo 1990). Given these considerations, it stands to reason that daily variation in patterns of activity may also coincide with similar variability in escape responses (Lattanzio 2014).

The speed of a predator's approach may also influence escape decisions (Stankowich and Blumstein 2005). For example, predator approach speed could serve as a cue to a prey species regarding whether or not it has been detected (Cooper Jr. 2006). In addition, faster approaches reduce the time until a predator reaches its potential prey, which affects their time to initiate an escape response as well as the likelihood of success of that response (Cooper Jr. 2003a, 2003b). The escape responses of lizards should be susceptible to variable predator approach speeds (Stankowich and Blumstein 2005), and some studies have shown that faster approaches do elicit a more-rapid prey response (e.g., greater FID, reviewed by Samia *et al.* 2015; but see Lattanzio 2009). Unlike FID, however, FD may not be as sensitive to variation in predator approach speed (e.g., Lattanzio 2009).

Here I describe variation in the escape behavior (FID and FD) of adult male emerald basilisk (*Basiliscus plumifrons* Cope, 1875; Figure 1) lizards in northeastern Costa Rica with respect to two factors, time of day (morning or early afternoon) and speed of approach (slow or fast). Both factors are known to influence the escape behavior in other lizard species (Cooper Jr. 2003a, 2006, Lattanzio 2014). I use time of day as a proxy for basilisk activity in this study because their activity exhibits a bimodal distribution with respect to time of day at my study site, with an initial peak in the early morning, followed by a suppression of activity until peaking again in the late afternoon hours (Lattanzio and LaDuke 2012). In accordance with theory (Ydenberg and Dill 1986), and the findings of previous studies (Cooper Jr. *et al.* 2006, Lattanzio and LaDuke 2012), I predicted that those *B. plumifrons* approached in the early afternoon, and those approached at a faster speed, would flee earlier and further.



Figure 1. Male emerald basilisk (*Basiliscus plumifrons*) from El Zota Biological Field Station in Costa Rica. Photograph by Matthew S. Lattanzio.

Materials and Methods

The Emerald Basilisk (*Basiliscus plumifrons*; Figure 1) is one of four currently recognized species of basilisk lizard (Corytophanidae: *Basiliscus*; see Maturana 1962). These species have a scattered, often overlapping distribution along the rainforests of Central and South America. *Basiliscus plumifrons* is a medium-sized, semi-arboreal lizard common throughout lowland moist forests of Costa Rica, Nicaragua, Panama, and Honduras (Wilson *et al.* 2013). Although primarily insectivorous, adult basilisks have been observed to also eat fruit, flowers, and even smaller vertebrates (Hirth 1963). Juvenile basilisks are commonly found along rivers, streams, lakes, and other waterways, where they can best make use of their unique escape strategy of running across water surfaces (Savage 2002). Adults, which are unable to use this behavior as effectively as juveniles (Hsieh and Lauder 2004), are often observed in areas greater than 30 m from water sources at this site (Lattanzio, pers. obs.).

I observed the escape responses of 17 adult male (> 115 mm snout–vent length; Laerm 1974) *B. plumifrons* from 19–24 July 2005 at El Zota Biological Field Station in Costa Rica (10.55728° N, 83.73628° W) (Pruetz and LaDuke 2001).

Males are easily discerned from females by the presence of dorsal and caudal crests (males-only, see Figure 1). This station encompasses approximately 1000 ha of a mosaic of primary and secondary rainforest habitats. Basilisks frequent secondary and edge habitats throughout the southeastern portion of El Zota (Lattanzio and LaDuke 2012). I therefore conducted this study along trail and road edges within the station.

I used binoculars to initially sight lizards from a distance (>10 m) to minimize disturbing my focal animals prior to data collection. In addition, I only approached lizards that were not already moving to minimize error in distance measurements. Upon locating a focal lizard, I then acted as a simulated predator by walking a direct, straight path towards the animal. I recorded FID and FD to the nearest 0.1 m using a tape measure.

I investigated the effect of two parameters likely to influence antipredator decisions on the escape responses of *B. plumifrons*: time of day and approach speed (Cooper Jr. 2003a, Lattanzio 2014). To investigate how time of day affects *B. plumifrons* escape decisions, I approached lizards either during the morning (08:00–10:00 h, $N = 8$ lizards) or early afternoon (12:00–14:00 h, $N = 9$ lizards). All lizards were perched on similar substrates (branches of small shrubs) prior to my approach. I chose these survey periods based on observations from a concurrent study on the bimodal daily activity patterns of other *B. plumifrons* lizards in this area: adult activity peaks closer to dawn and dusk later in July (Lattanzio and LaDuke 2012). My time periods therefore provide a useful contrast of *B. plumifrons* activity, with a period of high (morning) and low (early afternoon) activity. I approached lizards at one of two practiced, controlled paces: slow (~ 50 m/min) or fast (~ 150 m/min), following Lattanzio (2009). I conducted all surveys on sunny days, wore similarly-colored clothing throughout my experiment, and never explored the same area twice to avoid pseudoreplication.

All analyses were conducted within the R software environment (R Development Core Team 2012). Using Shapiro-Wilk's tests (function 'shapiro.test' in the stats package), I found that raw FID ($W = 0.91$, $p = 0.11$), but not FD ($W = 0.7$, $p < 0.001$), met assumptions of normality. In addition, FID and FD were uncorrelated [Spearman's rho (function 'cor.test' in stats package), $\rho = -0.38$, $S = 1126$, $N = 17$, $p = 0.13$]. I therefore analyzed each escape response (FID, FD) in a separate test. For FID, I used a factorial analysis of variance (ANOVA, function 'aov' in stats package) with time of day (morning or early afternoon) and approach speed (slow or fast) as fixed effects. I ranked values of FD using the function 'rank' in the base R package; these ranked FID values satisfied normality assumptions (Shapiro-Wilks test, $W = 0.96$, $p = 0.67$). I then applied a factorial ANOVA on the ranked FD values against the same predictors included in the FID model. I interpreted outputs of both models using Type II ANOVA tables via the function 'Anova' in the car package (Fox and Weisberg 2011). Residuals from both models satisfied normality assumptions (Shapiro-Wilks test, FID model: $W = 0.97$, $p = 0.8$; FD model: $W = 0.94$, $p = 0.33$). I also confirmed homogeneity of variances for each model using the function 'leveneTest' in the car package (Fox and Weisberg 2011) (FID model: $F_{3,13} = 0.52$, $p = 0.68$; FD model: $F_{3,13} = 0.27$, $p = 0.84$). Means are presented ± 1 standard deviation in text.

Results

In general, males approached in the morning had lower FID values than males approached in the early afternoon (morning FID = 2.85 ± 0.9 m; early afternoon FID = 4.64 ± 1.6 m). Approach speed, however, had little if any impact on lizard FID (slow pace FID = 3.72 ± 1.2 m; fast pace FID = 3.89 ± 2 m). My model supported a significant effect of time of day on male FID (time of day: $F_{1,13} = 7.04$, $p = 0.02$; approach speed: $F_{1,13} = 0.23$, $p = 0.64$; time of

day \times approach speed: $F_{1,13} = 0.73$, $p = 0.41$), with males fleeing sooner in the early afternoon than in the morning hours (Figure 2). In terms of FD, males approached in the morning appeared to flee further than males approached in the early afternoon (morning FD = 2.63 ± 1.9 m; early afternoon FD = 1.73 ± 0.7 m). Approach speed also appeared to impact FD, with faster approach coinciding with greater FD (slow pace FD = 1.86 ± 0.7 m; face pace FD = 2.48 ± 1.9 m). However, my model revealed that neither time of day nor approach speed had a significant effect on FD (time of day: $F_{1,13} = 1.1$, $p = 0.31$; approach speed: $F_{1,13} = 0.02$, $p = 0.88$; time of day \times approach speed: $F_{1,13} = 1.42$, $p = 0.26$).

Discussion

Basilisks, like other ambush foraging lizards, budget the energetic demands of territorial patrol and foraging behavior with alternative needs, such as antipredator behavior (Watters 2009). I quantified a component of antipredator behavior, the escape response, of adult male emerald basilisk lizards with respect to variation in time of day and approach speed, both of which may influence perceived risk in lizards (Cooper Jr. 2006, Lattanzio 2014). Despite my predictions, I found no effect of approach speed on flight initiation distance, and no effect of either time period or speed on distance fled. However, my prediction regarding the influence of time of day on flight initiation distance was supported, as lizards fled sooner in the early afternoon than in the morning hours (see Figure 2). Because the time periods of surveys used in my study correspond directly to a peak (morning) and valley (early afternoon) in *B. plumifrons* activity at my study site (Lattanzio and LaDuke 2012), these findings suggest that adult activity levels may affect risk perception in this species.

The type of activity exhibited by a prey organism during a predator's approach, and its energetic benefits, should influence the threshold of risk associated with the decision of when to initiate an escape response. However, the

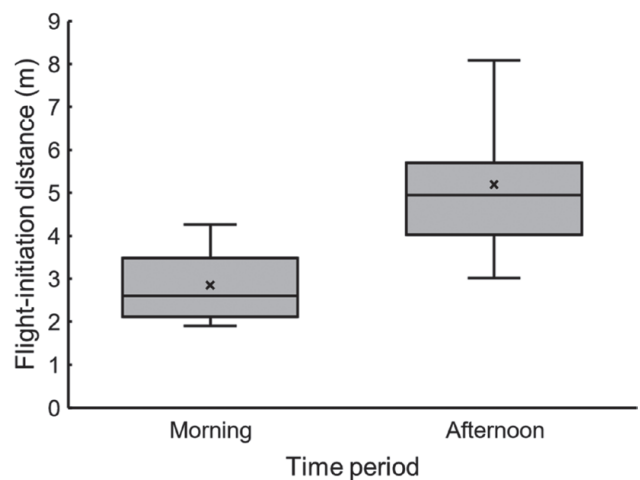


Figure 2. Variation in flight-initiation distance (in meters) by time of day, morning (08:00–10:00 h) or early afternoon (12:00–14:00 h) by adult *B. plumifrons* observed in this study. Medians are represented by the black central horizontal bar and means are indicated by the symbol 'x'.

influence of non-antipredator behaviors on escape decisions has received scant attention compared to other driving factors like the characteristics of a predator's approach (reviewed by Stankowich and Blumstein 2005). Thus far, both social and foraging activity have been found to influence flight-initiation distance in lizards (Cooper Jr. *et al.* 2006, Cooper Jr. 2009). Moreover, in another tropical lizard species, *Holcosus festivus* (Lichtenstein and Martens, 1856) (= *Ameiva festiva*), daily patterns of general activity also seem to have an impact on escape response thresholds throughout the day (Lattanzio 2014). In this study, I found that *B. plumifrons* lizards allowed a closer approach during periods of peak activity (morning), which supports that activity may influence escape behavior.

Interestingly, these findings contrast with escape patterns observed in a previous study on an active-foraging species, *H. festivus* (Lattanzio 2014). Unlike ambush foragers like *B. plumifrons* which move infrequently and remain perched for extended periods of time while scanning for

potential food, mates, or territory intruders, active foragers like *H. festivus* exhibit frequent and sporadic movement that increases their risk of drawing unwanted attention from nearby predators (Broom and Ruxton 2005). Thus, during periods of peak activity, species differing in foraging strategies should also differ in whether they flee sooner (active foragers) or later (ambush foragers) once an approaching predator is detected (Lattanzio 2014). In support of this hypothesis, *B. plumifrons* in this study allowed closer approaches during the morning, one of two periods during the day where they exhibit heightened periods of activity this time of year (see Lattanzio and LaDuke 2012). Much of the activity of this species at El Zota appears to be temperature-dependent, as activity period peaks shift throughout the summer months to cooler morning and late afternoon time periods (Lattanzio and LaDuke 2012). My current findings suggest that their daily patterns of escape response thresholds may shift as well. However, it is important to also recognize the influence of temperature on both lizard activity in general and, at least in some species, escape responses (Rocha and Bergallo 1990, Adolph and Porter 1993). For example, during periods of warmer air temperatures (such as afternoon hours), activity may be suppressed to conserve energy (Kearney 2013). By that logic, a delayed escape response should also be beneficial under these conditions to minimize the energetic costs of movement until predator attack is imminent.

One means to gain preliminary insight into the relative influence of activity patterns and temperature on escape responses would be to record air and substrate temperatures during an escape study and include those variables in data analyses as covariates. To that end, the results of previous studies are mixed with respect to the potential effect of temperature on escape responses, suggesting any effect may be species-specific and not universal (Blamires 1999, Stankowich and Blumstein 2005, Braun *et al.* 2010). It is important to note that I did not record air or substrate temperature data during my

approaches, so any conclusions about the direct association of these environmental conditions (or others) with lizard escape behavior would be speculative. I thus encourage others to consider thermal ecology of *B. plumifrons* in future escape studies to better disentangle the role of activity patterns versus thermal constraints on shaping diel variation in their escape decisions. Additional data on both active and ambush foraging species alike will also provide important insight into the extent that any differences in their escape tactics, or relationships between their escape behavior and activity patterns or temperature, mirror their divergent foraging strategies.

Unlike time of day, I found no effect of the speed of my approach on any escape responses of *B. plumifrons*. Numerous studies support that approach speed can be an important risk factor affecting the escape responses of multiple species (e.g., Cooper Jr. 1997, 2003a, Cooper Jr. and Whiting 2007a, 2007b, Cooper Jr. *et al.* 2009, but see also Lattanzio 2009). My methods are consistent with other studies (e.g., practiced approach speeds, similarly-colored clothing worn during all trials, etc.), and my approach speeds fall within the range of other published studies (broader range: 40–180 m/min; e.g., Cooper Jr. 1997, 2003a), suggesting that a lack of response to approach speed by *B. plumifrons* is likely not due to sampling error. Alternatively, because ambush foragers like *B. plumifrons* rely on crypsis to avoid predator detection and move infrequently, it may simply be that escape responses are a primary function of detection by (rather than the speed of) an approaching predator for these taxa (Broom and Ruxton 2005). However, given the relatively small sample size of my study, more work is needed to evaluate this claim.


In general, faster approach speeds are expected to elicit sooner prey responses (and thus greater flight-initiation distances) because a fast-approaching predator has likely detected the prey (e.g., Cooper Jr. 1997). However, this cue may be more important for active foragers whose

frequent movement alone may attract predator attention, compared to ambush foragers that rely on crypsis or proximity to a refuge to minimize detection (Cooper Jr. 2005). Moreover, it is also important to note that models predicting strategies for cryptic prey argue that slower, not faster, predator search speeds should elicit an earlier escape response (Broom and Ruxton 2005). Taken together, these studies suggest that prey responses may be complex and depend upon whether the prey perceives a positive correlation between approach speed and detection probability (Cooper Jr. 1997, Broom and Ruxton 2005), which may be limited to actively-foraging taxa.

Thus far, support for this foraging mode hypothesis remains mixed. In general, the responses of many active foraging species support a clear effect of approach speed on flight initiation distance: *Cnemidophorus murinus* (Laurenti, 1768) (Cooper Jr. *et al.* 2003); *Cordylus niger* Cuvier, 1829 (Cooper Jr. and Whiting 2007b); *Dipsosaurus dorsalis* (Baird and Girard, 1852) (Cooper Jr. 2003a); *Eumeces laticeps* (Schneider, 1801) (Cooper Jr. 1997); *Podarcis lilfordi* (Günther, 1874) (Cooper Jr. *et al.* 2009); *Psammodromus algirus* (Linnaeus, 1758) (Martín and López 1996); *Rhoptropus Boultoni* Schmidt, 1933 (Cooper Jr. and Whiting 2007a); *Trachylepis acutilabris* (Peters, 1862) (= *Mabuya acutilabris*) (Cooper Jr. and Whiting 2007a); and *Trachylepis sparsa* (Mertens, 1954) (Cooper Jr. and Whiting 2007b). However, of seven ambush foraging species studied to date, only three species fit expectations and were unaffected by approach speed: *Anolis limifrons* Cope, 1862 (= *Norops limifrons*) and *Anolis humilis* Peters, 1863 (= *Norops humilis*) (Lattanzio 2009); and *B. plumifrons* (this study). The responses of the other four ambush-foraging species (*Agama planiceps* Peters, 1862; *Anolis lineatopus* Gray, 1840; *Holbrookia propinqua* Baird and Girard, 1852; and *Sceloporus virgatus* Smith, 1938) fled sooner when approached at a faster pace (Cooper Jr. 2003b, 2005, 2006, Cooper Jr. and Whiting 2007a).

In truth, unlike approach speed, the distance between a predator and prey has consistent and strong fitness implications, regardless of other risk factors: as this distance approaches zero, the risk of mortality for a prey animal rises rapidly towards 100%. Thus, for cryptic prey species, distance to a predator may be a stronger cue for the initiation of an escape response than the speed of a predator's approach. One outcome of this consideration would be the prey animal eliciting similar escape responses regardless of predator approach speed variation, as was observed for *B. plumifrons* in the current study. There may also be a regional effect, as both Lattanzio (2009) and this study were conducted at the same field station (but on different species in different portions of the station property). Thus, lizards may be more accustomed to human presence at El Zota than they would be in other areas (e.g., Labra and Leonard 1999, Diego-Rasilla 2003, Prosser *et al.* 2006). Data on a wider array of taxa along a broader gradient of human disturbance would be useful in this respect to better understand the implications of predator approach characteristics for prey behavior.

Acknowledgments

I thank Thomas LaDuke as well as DANTA Association for Conservation of the Tropics for providing access to the field site and materials used to conduct this study. I also respectfully acknowledge the station workers, José, Ana, and their family at El Zota Biological Field Station for their on-site assistance and accommodations. I am further indebted to Casey Fox and John Scrivo for assistance in the field. This work was conducted in full compliance with all applicable institutional animal care and use guidelines set forth by East Stroudsburg University, and under a wildlife research permit issued to my advisor (TCL) by the Costa Rican Ministerio del Ambiente, Energía y Telecomunicaciones. 

References

- Adolph, S. C. and W. P. Porter. 1993. Temperature, activity, and lizard life histories. *American Naturalist* 142: 273–295.
- Blamires, S. J. 1999. Factors influencing the escape response of an arboreal agamid lizard of tropical Australia (*Lophognathus temporalis*) in an urban environment. *Canadian Journal of Zoology* 77: 1998–2003.
- Braun, C. A., T. A. Baird, and J. K. LeBeau. 2010. Influence of substrate temperature and directness of approach on the escape responses of juvenile collared lizards. *Herpetologica* 66: 418–424.
- Brock, K. M., P. A. Bednekoff, P. Pafilis, and J. Foufopoulos. 2015. Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): the sum of all fears? *Evolution* 69: 216–231.
- Broom, M. and G. D. Ruxton. 2005. You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology* 16: 534–540.
- Cooper Jr., W. E. 1997. Factors affecting risk and cost of escape by the broad-headed skink (*Eumeces laticeps*): predator speed, directness of approach, and female presence. *Herpetologica* 53: 464–474.
- Cooper Jr., W. E. 2003a. Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. *Canadian Journal of Zoology* 81: 979–984.
- Cooper Jr., W. E. 2003b. Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology* 109: 617–626.
- Cooper Jr., W. E. 2005. When and how do predator starting distances affect flight initiation distances? *Canadian Journal of Zoology* 83: 1045–1050.
- Cooper Jr., W. E. 2006. Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology* 112: 858–864.
- Cooper Jr., W. E. 2009. Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behavioral Ecology and Sociobiology* 63: 1765–1771.
- Cooper Jr., W. E. and D. T. Blumstein. 2015. *Escaping from Predators: an Integrative View of Escape Decisions*. Cambridge. Cambridge University Press. 460 pp.
- Cooper Jr., W. E. and W. G. Frederick. 2007. Optimal flight initiation distance. *Journal of Theoretical Biology* 244: 59–67.
- Cooper Jr., W. E. and V. Pérez-Mellado. 2004. Tradeoffs between escape behavior and foraging opportunity by the Balearic lizard (*Podarcis lilfordi*). *Herpetologica* 60: 321–324.
- Cooper Jr., W. E., D. Hawlena, and V. Pérez-Mellado. 2009. Islet tameness: escape behavior and refuge use in populations of the Balearic lizard (*Podarcis lilfordi*) exposed to differing predation pressure. *Canadian Journal of Zoology* 87: 912–919.
- Cooper Jr., W. E., V. Pérez-Mellado, and D. Hawlena. 2006. Magnitude of food reward affects escape behavior and acceptable risk in Balearic lizards, *Podarcis lilfordi*. *Behavioral Ecology* 17: 554–559.
- Cooper Jr., W. E., V. Pérez-Mellado, T. Baird, T. A. Baird, J. P. Caldwell, and L. J. Vitt. 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behavioral Ecology* 14: 288–293.
- Cooper Jr., W. E. and M. J. Whiting. 2007a. Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. *Ethology* 113: 661–672.
- Cooper Jr., W. E. and M. J. Whiting. 2007b. Effects of risk on flight initiation distance and escape tactics in two southern African lizard species. *Acta Zoológica* 53: 446–453.
- Diego-Rasilla, F. J. 2003. Human influence on the tameness of wall lizard, *Podarcis muralis*. *Italian Journal of Zoology* 70: 225–228.
- Fox, J. and S. Weisberg. 2011. Car: companion to applied regression. R package Version 2.0-2. URL: <http://CRAN.R-project.org/package=car>.
- Hirth, H. F. 1963. The ecology of two lizards on a tropical beach. *Ecological Monographs* 33: 83–112.
- Hsieh, S. T. and G. V. Lauder. 2004. Running on water: three-dimensional force generation by basilisk lizards. *Proceedings of the National Academy of Sciences USA* 101: 16784–16788.
- Kearney, M. R. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters* 16: 1470–1479.
- Labra, A. and R. Leonard. 1999. Intraspecific variation in antipredator response of three species of lizards (*Liolaemus*): possible effects of human presence. *Journal of Herpetology* 33: 441–448.

- Laerm, J. 1974. A functional analysis of morphological variation and differential niche utilization in basilisk lizards. *Ecology* 55: 404–411.
- Lailvaux, S. P., G. J. Alexander, and M. J. Whiting. 2003. Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. *Physiological and Biochemical Zoology* 76: 511–521.
- Lattanzio, M. S. 2009. Escape tactic plasticity of two sympatric *Norops* (Beta *Anolis*) species in northeast Costa Rica. *Amphibia-Reptilia* 30: 1–6.
- Lattanzio, M. S. 2014. Temporal and ontogenetic variation in the escape response of *Ameiva festiva* (Squamata, Teiidae). *Phyllomedusa* 13: 17–27.
- Lattanzio, M. S. and T. C. LaDuke. 2012. Habitat use and activity budgets of emerald basilisks (*Basiliscus plumifrons*) in northeast Costa Rica. *Copeia* 2012: 465–471.
- Martín, J. 2003. Changes in the escape responses of the lizard *Acanthodactylus erythrurus* under persistent predatory attacks. *Copeia* 2003: 408–413.
- Martín, J. and P. López. 1996. The escape response of juvenile *Psammodromus algirus* lizards. *Journal of Comparative Psychology* 110: 187–192.
- Maturana, H. R. 1962. A study of the species of the genus *Basiliscus*. *Bulletin of the Museum of Comparative Zoology* 128: 1–34.
- Prosser, C., S. Hudson, and M. B. Thompson. 2006. Effects of urbanization on behavior, performance, and morphology of the Graden Skink, *Lampropholis guichenoti*. *Journal of Herpetology* 40: 151–159.
- Pruetz, J. D. and T. C. LaDuke. 2001. New field site: preliminary census of primates at El Zota Biological Field Station, Costa Rica. *Neotropical Primates* 9: 22–23.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org>.
- Rocha, C. F. D. and H.G. Bergallo. 1990. Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. *Ethology Ecology and Evolution* 2: 263–268.
- Samia, D. S. M., D. T. Blumstein, T. Stankowich, and W. E. Cooper Jr.. 2015. Fifty years of chasing lizards: new insights advance optimal escape theory. *Biological Reviews* 91: 349–366.
- Savage, J. M. 2002. *The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas*. Chicago. University of Chicago Press. 954 pp.
- Stankowich, T. and D. T. Blumstein. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London B, Biological Sciences* 272: 2627–2634.
- Stellatelli, O. A., C. Block, L. E. Vega, and F. B. Cruz. 2015. Nonnative vegetation induces changes in predation pressure and escape behavior of two sand lizards (Liolaemidae: *Liolaemus*). *Herpetologica* 71: 136–142.
- Vanhooydonck, B., A. Herrel, and D. J. Irschick. 2007. Determinants of sexual differences in escape behavior in lizards of the genus *Anolis*: a comparative approach. *Integrative and Comparative Biology* 47: 200–210.
- Watters, J. L. 2009. Daily activity budgets for neonate and adult *Sceloporus jarrovi* and adult *Sceloporus virgatus* in southeastern Arizona. *Journal of Herpetology* 43: 665–675.
- Wilson, L. D., J. H. Townsend, and W. Lamar. 2013. *Basiliscus plumifrons*. *The IUCN Red List of Threatened Species* 2013: e.T203046A2759302.
- Ydenberg, R. S. C. and L. M. Dill. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16: 229–249.

Editor: Claudia Koch