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Escape behavior in gravid and non-gravid females of *Gonatodes albogularis* (Squamata: Sphaerodactylidae)

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Abstract

Escape behavior in gravid and non-gravid females of *Gonatodes albogularis* (Squamata: Sphaerodactylidae). Theoretical models of predator-prey relationships describe tradeoffs between energetic and other costs of escape, effectiveness of escape behavior, and predation risk. These models predict that an animal will flee when the expected fitness cost due to risk of predation becomes equal to the the cost of the escape or post-encounter fitness is maximized, depending on the model. In this framework, several individual and ecological variables have been shown to affect escape patterns, but the effect of reproductive status has been studied in few species. We assess differences in escape behavior between gravid and non-gravid females of *Gonatodes albogularis*. Lizards were surveyed by applying a free search method along independent transects. For each lizard, we determined reproductive status as gravid or non-gravid and recorded several variables related to escape behavior. We made a discriminant function analysis to see whether the state of individuals affect escape behavior. Our results show that the escape variables distance fled, the final distance and the distance to refuge differ between gravid and non-gravid females. These findings support predictions based on risk and cost, but do not support models of flight initiation distance. Such differences could be related to a physiological process known as behavioral compensation, through which some individuals (gravid females in our case) modify their behavior to offset predation risk. Further studies are needed to see if behavioral compensation can be explained in terms of adaptive processes in *G. albogularis*.

Keywords: behavioral compensation, escape theory, escape behavior, predation risk.

Resumo

Comportamento de fuga em fêmeas grávidas e não-grávidas de *Gonatodes albogularis* (Squamata: Sphaerodactylidae). Modelos teóricos de relações predador-presa descrevem balanços entre custos de fuga (energéticos e de outros tipos), eficiência do comportamento de fuga e risco de

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predação. Esses modelos preveem que um animal escapará quando o custo esperado em termos de sucesso reprodutivo devido ao risco de predação quando for igual ao custo de fuga ou quando o sucesso reprodutivo após o encontro for maximizado, dependendo do modelo. Nesse cenário, demonstrou-se que diversas variáveis individuais e ecológicas afetam os padrões de fuga, mas o efeito do status reprodutivo foi estudado em poucas espécies. Nós avaliamos diferenças no comportamento de fuga entre fêmeas grávidas e não-grávidas de *Gonatodes albogularis.* Os lagartos foram estudados aplicando-se um método de procura livre ao longo de transectos independentes. Para cada fêmea, determinamos o status reprodutivo como grávida ou não-grávida e registramos diversas variáveis relacionadas ao comportamento de fuga. Desenvolvemos uma análise discriminante para verificar se o estado dos indivíduos afetavam o comportamento de fuga. Nossos resultados mostram que as variáveis distância percorrida na fuga, distância final e distância para o refúgio diferem entre fêmeas grávidas e não-grávidas. Essas descobertas sustentam previsões baseadas em risco e custo, mas não sustentam modelos de distância de início de fuga. Tais diferenças poderiam estar relacionadas como um processo conhecido como compensação comportamental, por meio do qual alguns indivíduos (as fêmeas grávidas, no nosso caso) modificam seu comportamento para compensar risco de predação. Estudos adicionais são necessários para verificar se a compensação comportamental pode ser explicada em termos de processos adaptativos em *G. albogularis.*

Palavras-chave: compensação comportamental, comportamento de fuga, risco de predação, teoria da fuga.

Introduction

Interest in predator-prey interactions has led to the development of theoretical models, which assess the fitness costs of escape behavior in relation to the predation risk (Ydenberg and Dill 1986, Cooper and Frederick 2007). These models posit that an animal will flee when the risk of predation becomes equal to the cost of escape (Ydenberg and Dill 1986) or at the distance where expected fitness after the encounter is maximized (Cooper and Frederick 2007). Despite this quantitative difference in predictions, the two models make qualitatively identical predictions that the distance from a predator at which escape begins decreases as the cost of fleeing increases. Escape costs are primarily loss of opportunities to enhance fitness by engaging in other activities such as feeding or reproduction, but also include minor energetic costs (Martín and López 1999, Martín *et al.* 2003, Cooper and Pérez-Mellado 2004).

In addition to considering distance between prey and predator, these models also consider distance to a refuge (Bulova 1994) and allow predictions about the effects of numerous factors that can affect the escape behavior in lizards, including the microhabitat (Martín and López 1995, 2000, Cooper 1999, Cuadrado *et al.* 2001), size of the perch (Losos and Irschick 1996), thermal conditions (Carrascal *et al.* 1992, Stankowich and Blumstein 2005, Dominguez-López *et al.* 2015a), movement capabilities (Martín and López 1995, Domínguez-López *et al.* 2015b) and reproductive behavior or reproductive costs (Shine 1980, Bauwens and Thoen 1981, Schwarzkopf and Shine 1992a).

The reproductive state of individuals can affect escape success by a reduction in locomotion capabilities (e.g., reduced speed related to a higher weight in gravid females) (Bauwens and Thoen 1981, Brodie 1989, Schwarzkopf and Shine 1992a, Sinervo and DeNardo 1996). Several studies showed a higher vulnerability to predators by gravid rather than non-gravid females (e.g., Shine 1980, Bauwens and Thoen 1981, Seigel *et al.* 1987, Brodie 1989, Van Damme *et al.* 1989, Cooper *et al.* 1990, Schwarzkopf and Shine 1992a, Qualls and Shine 1997). Because reproductive state has a survival cost, some species have developed behavioral mechanisms to compensate for a reduction in locomotor capabilities (e.g., associated with gravidity) by increasing escape success when facing predators.

Behavioral compensation therefore, decreases cost associated with a reduction in escape success (Langkilde *et al.* 2005). In lizards, behavioral compensation can involve more time basking or foraging to compensate for increased energy requirements while regenerating autotomized tails (Dial and Fitzpatrick 1981), spending more time in refuge to compensate for increased predation risk (e.g., after tails have been autotomized) (Martín and Salvador 1993, Langkilde *et al.* 2005). Because behavioral compensation affects lizards' survival, it is of great relevance to demography. However, it has been little studied in Neotropical species.

The Yellow-head Gecko, *Gonatodes albogularis* (Duméril and Bibron, 1836), inhabits dry and wet tropical forests (Rivero-Blanco 1979, Köhler 2003, Schargel 2008). It occurs in several microhabitats including tree trunks, rock caves and foliage. It natural predators include larger lizards, some snake species, raptors, certain other birds and some mammals (Fitch 1973, Bello 2000). *Gonatodes albogularis* is diurnal with reproductive activity all year round. Females have an acyclical and asynchronous reproductive period and an invariable clutch size of one egg (Serrano-Cardozo *et al.* 2007). In this study we assess differences in escape behavior between gravid and non-gravid females of *G. albogularis.* We hypothesize that reproductive state, affects escape behavior of females *G. albogularis* regardless of modifying influences of individual differences in mass or size.

Materials and Methods

Study Site

The area is one of the last relicts of tropical forest located in the south of the Córdoba Department, Colombia (08°04'48.7" N, 75°42'28.4" W). We conducted our study in the Choco-Magdalena region, characterized as Dry Tropical Forest, with mean annual temperature of 28°C and seasonal rains (Hernández-Camacho *et al.* 1992).

Surveys

Fieldwork was conducted in March and April 2012, coincident with the period of highest activity reported for this species (Serrano-Cardozo *et al.* 2007). We surveyed lizards using a free search method, walking along parallel line transects (with a separation of 10 m between them) from 09:00 to 17:00 h. When an individual was found, one observer (always the same) simulated a predatory attack by approaching the gecko directly, at the same speed (1 m/s) until it fled. The distance between the researcher and the lizard when the researcher began to approach was 5 m. The approaching researcher stopped moving as soon as the lizard started to flee and remained still until the lizard stopped fleeing. For each observation we recorded the following variables: flight initiation distance (FID): distance between the lizard and the observer in the moment when escape started; distance fled (DF): distance between the first location of the lizard and its location at first stop after escaping; final distance (FD): distance between the observer and the point at which the lizard stopped moving or the point at which the lizard went into hiding; distance to refuge (DR): distance between the first location of the lizard and the closest shelter (ground caves, rocks, trunks, or foliage) (Bauwens and Thoen 1981, Bulova 1994, Vanhooydonck *et al.* 2007). Quantitative data were recorded using a tape measure with 1 cm accuracy.

While one observer recorded escape variables, the second observer captured the individual and recorded snout–vent length (SVL) and tail length (TL), using a dial caliper with 0.1 mm accuracy; mass (M), using a scale with 0.01 g accuracy; sex, on the basis of external features; age, classified as adult and juvenile on the basis of the minimum size at sexual maturity (30.1

mm for males and 31.7 mm for females; Serrano-Cardozo *et al.* 2007); and reproductive state of females, classified as gravid and non-gravid, on the basis of external features. Females were identified as gravid by the presence of an egg, which can be easily recognized by examining the abdominal side visually and by palpation (Domínguez-López pers. com.).

Data Analysis

We used a combination of multivariate analysis, ANCOVA and Generalized Linear Models (GLM), to assess whether the individual state (gravid and non-gravid) affects escape behavior. However, because escape behavior might be also related to individuals' variables such as SVL, TL and/or M, we firstly tested for differences in these variables between gravid and non-gravid females, using Two-tailed Student t-test. Because M showed differences between females' states, we included it as a covariable in the analyses.

To assess the differences in escape behavior between females' states in a broad sense, we performed a multivariate analysis using as covariates FID, DF, FD and DR. However, considering that states might be shaped by differences in M among individuals, we performed two discriminant analysis, with and without M as covariate, to see the contribution of escape variables in both cases.

We tested assumptions of homoscedasticity and normality for all the escape variables. In the case of FID and DF, we had to apply transformations to the data as logFID and log(DF+1) in order to meet assumptions. We then performed an ANCOVA to compare both FID and DF between gravid and non-gravid females, including M as a covariate. In the case of FID we also checked for a potential effect of DR, since this variable could be also shaping a state effect. Due that an ANCOVA showed that DR and FID have an interaction ($p < 0.05$), we decided to perform Generalized Linear Models (GLM) with a Gaussian distribution to assess if the individuals' state, M and/or DR significantly affect FID.

In the case of FD and DR, even transformed data failed in meeting the assumption of normality, thus we decided to apply GLM with a Gaussian distribution, to assess the relationship between these variables and individual's state plus M as explanatory variables. For all the tests, we considered a $p < 0.05$ as significant.

Results

We recorded escape data for 95 females, among which 37 were gravid and 58 non-gravid. We observed differences in all the escape variables measured when comparing between gravid and non-gravid females (Table 1). Considering the individual variables, a Two-tailed Student t-test showed significant differences in M between gravid and non-gravid females (t: 9.37; $p < 0.05$), but no differences in SVL (t: 0.47; $p = 0.64$) or in TL (t: 0.41; $p = 0.59$) were observed.

Both discriminant analyses showed a good separation between gravid and non-gravid females and the contribution of escape covariates where similar. In the analysis that considered M as covariate, the eigenvalue that represents the variation of the direction of greatest variation of the data was of 20.18 and reconstructed 100% of the total variability with a single canonical discriminant function given by $F = -8.57 - 2.89\text{DF} - 5.86\text{FD} + 6.42\text{FID} - 0.54\text{DR} + 0.59\text{M}$.

The centroids in the discriminant space show that the groups are opposed in the canonical axis at values of gravid = 5.57 and non-gravid = -3.55 and the cross-classification (Table 2) shows that the state allows to discriminate the observations in an almost perfect way since the classification given by the discriminant function coincides 100% with the one given by the state. From the discriminant function standardized by common covariances, it can be seen that M is the least important variable for discrimination, indicating that escape variables are the most important to separate both groups (Table 3).

Table 1. Mean ± SD values for the individual and escape variables assessed in both gravid (G = 37) and non-gravid (NG = 58) females. SVL, snout-vent length; M, mass; TL, tail length; FID, flight initiation distance; DF, distance fled; FD, final distance; DR, distance to refuge.

	Individual variables			**Escape variables**			
	SVL	M	TL	FID	DF	FD	DR
G	32.96 ± 0.7	4.85 ± 0.1	31.54 ± 0.5	3.93 ± 0.4	1.40 ± 0.1	2.00 ± 0.5	2.05 ± 0.6
NG	32.90 ± 0.7	4.33 ± 0.3	31.46 ± 0.5	2.48 ± 0.3	1.15 ± 0.2	1.46 ± 0.2	2.94 ± 0.5

Table 2. Cross-classification and apparent rate of error.

Group	Gravid	Non-gravid	Total	Error (%)
Gravid	37	0	37	0.00
Non-gravid	0	58	58	0.00
Total	**37**	**58**	**95**	**0.00**

Table 3. Discriminant functions data standardized by common covariances. FD, final distance; FID, flight initiation distance; DF, distance fled; DR, distance to refuge; M, mass.

Covariate	Relative importance
FD	-2.15
FID	2.13
DF	-0.42
DR	-0.28
M	0.16

Overall, the specific analyses performed for each escape variable indicated that FID, DF, and FD were significantly larger for gravid than for non-gravid females, while DR was significantly shorter in gravid females (Figure 1). In the case of FID and DF, ANCOVAs analyses showed that although M has an effect on escape behavior, significant differences between individual states exists, even after controlling for the effect of M, with values of $F = 214.75$ and $F = 400.07$ respectively ($p < 0.05$). A GLM showed that M does not affect FID ($p < 0.05$), but this variable is affected by state (gravid and non-gravid) and DR ($p < 0.05$). Similar results were obtained for FD and RD, where GLM analyses showed that variations in these variables were only explained by individual state (gravid and non-gravid) but not by M, with $p < 0.05$.

Discussion

Overall, our research confirms that reproductive status affects escape behavior in *G. albogularis.* Among the variables included in the discriminant model, the final distance and the flight initiation distance were the most important to separate gravid and non-gravid-females. Although the mass of individuals was different between states, this variable showed a poor support in separating groups with respect to the escape variables.

The differences observed between gravid and non-gravid females might be related to a physiological process known as behavioral compensation, through which some individuals (gravid females in our case) change their behavior to balance costs and benefits in avoiding predators (Cullum 1998, Ghalambor *et al.* 2004, Husak *et al.* 2006).

In lizards, gravid females have a clear disadvantage when facing predators in relation to non-gravid ones; the above is because when they become heavier, they become slower (Shine 1980, Van Damme *et al.* 1989). This decrease in escape abilities can be compensated ecologically by triggering escape earlier and/or by perching closer to shelter.

Values of FID in *G. albogularis* were larger in gravid than non-gravid females. These results are at opposite with studies in other reptile species, where gravid females delayed their

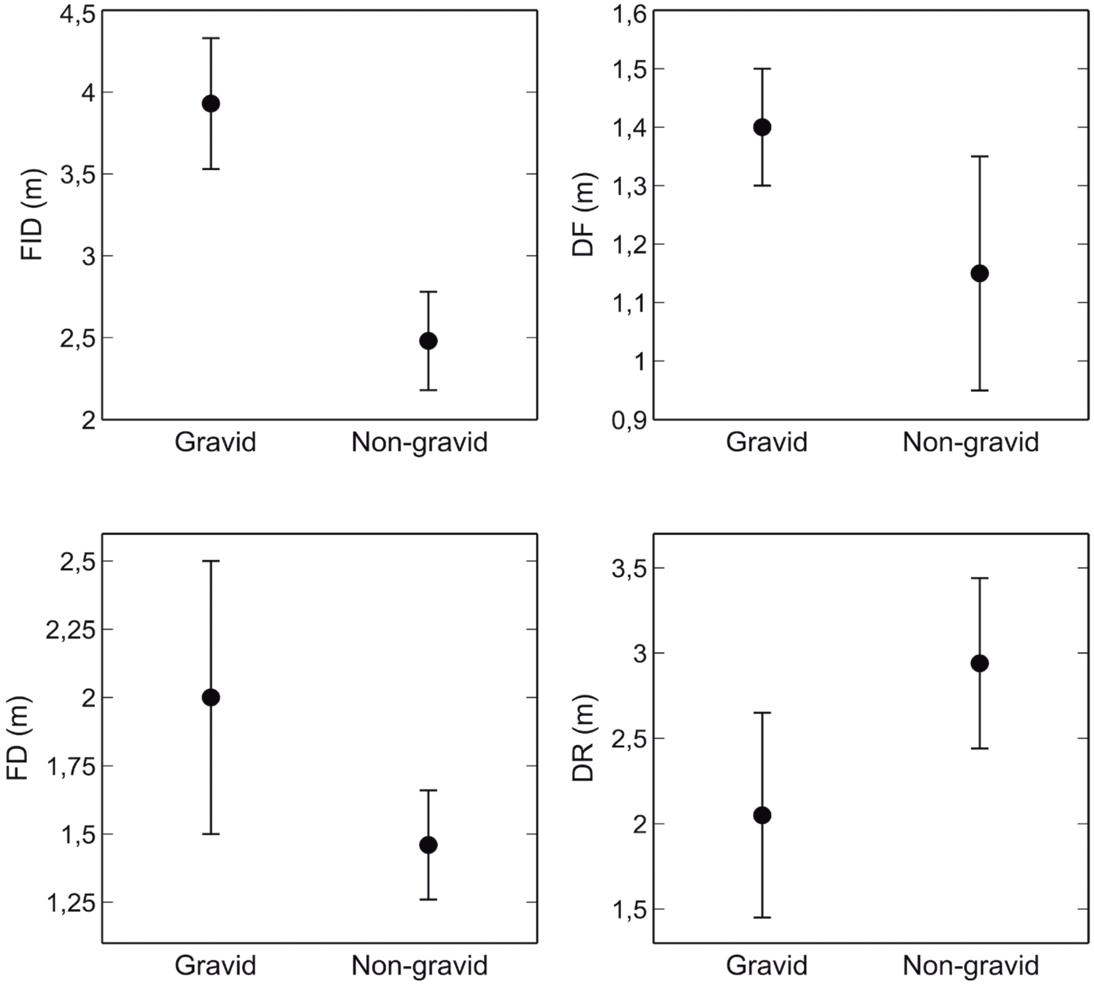

Figure 1. Comparison of escape behavior between gravid and non-gravid females. FID, flight initiation distance; DF, distance fled; FD, final distance; DR, distance to refuge. The data is presented as mean ± SD.

escape, allowing a closer FID (Braña1993, Blázquez 1995, Charland 1995, Charland and Gregory 1995). A larger FID allows a higher chance of avoiding predators' attacks, as seen in other studies (Bauwens and Thoen 1981, Schwarzkopf and Shine 1992a, b). Although not assessed in this study, we assume a behavioral compensation that might result from a decrease in velocity of gravid females, as seen in Bauwens and Thoen (1981) and Sinervo *et al.* (1991). Although this behavioral change could affect access to food and thermoregulation sites, the survival advantage likely outweighs costs (Shine 1980, Seigel *et al.* 1987, Sinervo *et al.* 1991, Lailvaux *et al.* 2003). Behavioral differences observed in non-gravid females most likely are related to reproduction, feeding, and microhabitat use. Our results support optimal escape theory proposed by Ydenberg and Dill (1986).

When confronted by a potential predator, gravid females ran further than non-gravid ones. It is possible that gravid females may run further to put a greater distance between them and the pursuit predator, which may provide a survival advantage that offsets the energetic cost of running a greater distance while carrying an egg. An alternative explanation might be that non-gravid females may not run as far because they can outpace a predator even if it gets close to them. This could be related to habitat structure and complexity, as seen in other studies (Martín and López 1995, 2000, Cooper 1999, Cuadrado *et al.* 2001). Yellow-headed geckos start to flee earlier in microhabitats lacking suitable refuges, especially when on rocks, but also on leaf litter (Domínguez-López *et al.* 2016). Moreover, although cryptic females could be undetected in leaf litter, this microhabitat is not a good refuge, because predators can locate a concealed prey there (Martín and López 2000, Capizzi *et al.* 2007). Previous observations on *G. albogularis* showed that females perch closer to shelter than males (Domínguez-López *et al.* 2015a) and that they prefer to pair with those males that offer microhabitats structurally more complex (Domínguez-López *et al.* 2016). Future studies should assess in more detail whether the observed differences are related to habitat complexity, reproductive state, or both.

Differences in escape behavior related to reproductive state have also been observed in other lizard species. For example, some sit-and-wait species use a lower amount of energy when feeding (contrary to widespread foragers) but not when facing predators, as seen in *Crotaphytus collaris* (Say, 1823) (Husak *et al.* 2006) and some female *Anolis* (Losos and Irschick 1996, Irschick 2000). Females may spend more energy in escaping than in feeding and probably this situation increases in gravid females. However, these gravid females could compensate these energetic costs by changing their behavior (Bauwens and Thoen, 1981, Brodie 1989, Cooper *et al.* 1990). In *G. albogularis,* further studies are needed for a deep understanding of the causes associated with the observed patterns and to determine whether behavioral compensation can be explained in terms of adaptive processes.

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