

Aggressive Behavior and Performance in the Tegu Lizard *Tupinambis merianae*

Anthony Herrel^{1,*}

Denis V. Andrade²

José Eduardo de Carvalho³

Ananda Brito⁴

Augusto Abe²

Carlos Navas⁴

¹Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France;

²Departamento de Zoologia, Universidade Estadual Paulista, Rio Claro, c. p. 199, São Paulo 13506-900, Brazil;

³Universidade Federal de São Paulo, Campus Diadema, Rua Prof. Artur Riedel 275, 09972-270, Diadema, São Paulo, Brazil; ⁴Departamento de Fisiologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14 No. 321, CEP 05508-900, São Paulo, Brazil

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ABSTRACT

Aggression is an important component of behavior in many animals and may be crucial to providing individuals with a competitive advantage when resources are limited. Although much is known about the effects of catecholamines and hormones on aggression, relatively few studies have examined the effects of physical performance on aggression. Here we use a large, sexually dimorphic teiid lizard to test whether individuals that show high levels of physical performance (bite force) are also more aggressive toward a potential threat (i.e., a human approaching the lizard). Our results show that independent of their sex, larger individuals with higher bite forces were indeed more aggressive. Moreover, our data show that individuals with higher bite forces tend to show decreased escape responses and are slower, providing evidence for a trade-off between fight and flight abilities. As bite force increased dramatically with body size, we suggest that large body size and bite force may reduce the threshold for an individual to engage in an aggressive encounter, allowing it to potentially gain or maintain resources and fight off predators while minimizing the risk of injury.

Introduction

Aggression is a fascinating phenomenon from a human perspective because aggression in society is considered to be a serious social problem (Simpson 2001). However, aggression is crucial for many organisms because more aggressive individuals are often better competitors for limited resources such as food, shelter, and mates. Moreover, aggression may be an important anti-predator strategy that may increase the survival of an organism. High levels of aggression, however, may also induce costs by reducing growth rate and condition (e.g., Civantos 2002), by increasing energy expenditure (Marler and Moore 1988), or by increasing risk of physical injury (Lappin and Husak 2005).

Body size has been invoked as an important factor mediating aggression, with larger individuals typically being more aggressive and more dominant than smaller ones (Chani 1995; Goldsmith et al. 1996; Nowbahari et al. 1999; Whiting et al. 2006; Hoyer et al. 2008; but see Morell et al. 2005; Just et al. 2007). However, one factor that has received little attention to date is the role of physical performance in establishing differences in aggression between individuals. Although several studies have demonstrated that dominant males have higher levels of locomotor performance than nondominant males (Robson and Miles 2000; Perry et al. 2004; but see Lopez and Martin 2002), this may be related to these individuals being better at patrolling or defending territories rather than being associated with aggression per se. Recently, an important role of bite force in determining the outcome of aggressive interactions in lizards has been suggested (Lailvaux et al. 2004; Huyghe et al. 2005; Lappin and Husak 2005; Husak et al. 2006). Moreover, in at least one species of lizard, high levels of bite-force capacity were associated with some aspect of fitness (number of offspring; Husak et al. 2009), suggesting that this trait may be under direct selection.

These findings raise the question of whether strong individuals (that are probably better fighters) are also more likely to fight in general; that is, is physical performance related to levels of aggression in general? Although this might be expected in a sex-specific context, because circulating testosterone levels directly affect aggression (Weiss and Moore 2004; Korzan et al. 2006; Kabelik et al. 2008) and muscle mass (Bardin and Catterall 1981; Joubert and Tobin 1995; Emerson 2000; Dorlöchter et al. 2004) as well as performance traits such as bite force (Husak et al. 2007), there are indications that testosterone may not play a role in predatory aggression (Simpson 2001). However, stronger individuals who are better fighters would be more likely to gain from engaging in an aggressive interaction irrespective of the context (i.e., during both predator-prey and intraspecific interactions) because the costs of engaging in an aggressive encounter are probably lower and the likelihood of winning a fight is higher.

* Corresponding author; e-mail:anthony.herrel@mnhn.fr.

Here, we investigate correlations between bite-force capacity and aggressive behavior for both sexes in a large, sexually dimorphic teiid lizard, *Tupinambis merianae*. Earlier studies have shown that male *T. merianae* will fight for access to territories and females, female *T. merianae* will fight over nesting sites (Chani 1995), and both sexes will fight over food resources (at least in captivity; D. V. Andrade, personal observation) and stand their ground to fight when confronted with predators (Von Ihering 1953, 2002; Santos 1981; de Lema 1983; Haddad et al. 2008), making aggression particularly relevant to study in this species.

Material and Methods

Animals and Husbandry

The animals were obtained from the Jacarezário at the Universidade Estadual Paulista (Rio Claro, São Paulo, in south-eastern Brazil), which runs a conservation breeding program for tegu lizards and other reptiles (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis reg. 1-35-94-1088-8). At this laboratory, the lizards are kept in small groups (5–10 individuals) in outdoor pens (5 m × 10 m or 2 m × 2 m) and are provided with water and ground shelters, as well as shade and sunny areas for thermoregulation. In spring and summer, the animals are fed three times a week with ground beef, fruits, and/or 1-d-old chickens.

Behavioral Trials

To assess the behavioral responses of animals, a series of four consecutive tests were conducted. Although the consecutive nature of the testing protocol is likely to bias the responses of the animals, we were primarily interested in comparing an identical treatment designed to elicit increased levels of aggression across individuals. This allowed us to test whether performance was associated with aggression at the individual level. All tests were conducted on three consecutive days between 10:00 a.m. and 6:00 p.m., when animals were fully active, by the same person wearing the same clothes. Because behavioral responses may be dependent on temperature (Hertz et al. 1982; Crowley and Pietruszka 1983; Mautz et al. 1992; Herrel et al. 2007), before testing, the temperatures of the lizards were measured from a distance using an infrared thermometer. Mean surface temperature of the lizards was $36.8^{\circ} \pm 3.44^{\circ}\text{C}$. The first test involved walking slowly, but deliberately, toward the animal in its home enclosure (familiar environment). While doing so, another person recorded (1) the distance from the animal to the observer at the first response of the animal, (2) the response type, and (3) whether the animals arched their back or not (0 or 1). Arching is a typical defensive behavior in these lizards that involves a pronounced arching of the back and a reorientation of the lizard in a direction facing the potential threat. Possible response types and scores were running away (1), walking away (2), ignoring (3), threatening (4), attacking and retreating (5), and attacking and holding ground for 10 s or more (6). Thus, higher scores were associated with more aggressive behaviors. For the second test, animals were caught, placed in

an unfamiliar environment (narrow corridor with a shelter consisting of *Philodendron selloum* leaves at the end), and approached by the same person after 1 min. As in the first test, the other person recorded the response type and whether animals arched their back or not, and a third person recorded the time before the animal retreated into the shelter. Next, animals were captured again and placed in 100-cm × 50-cm boxes with no shelter. After 1 min, the same person from the previous test approached the lizard with his hand (wearing a glove) and tried to touch the lizard. The other person recorded the number of aggressive bouts (threats or threat displays), the number of actual bites, and the number of escape bouts (animal running away from the hand). For the final test, the animal was captured and tapped gently on the side of the jaws while a third person recorded the behavioral response. The possible responses and scores were as follows: ignore or tongue flick (1), open-mouth threat (2), attempt to bite (3), or successful

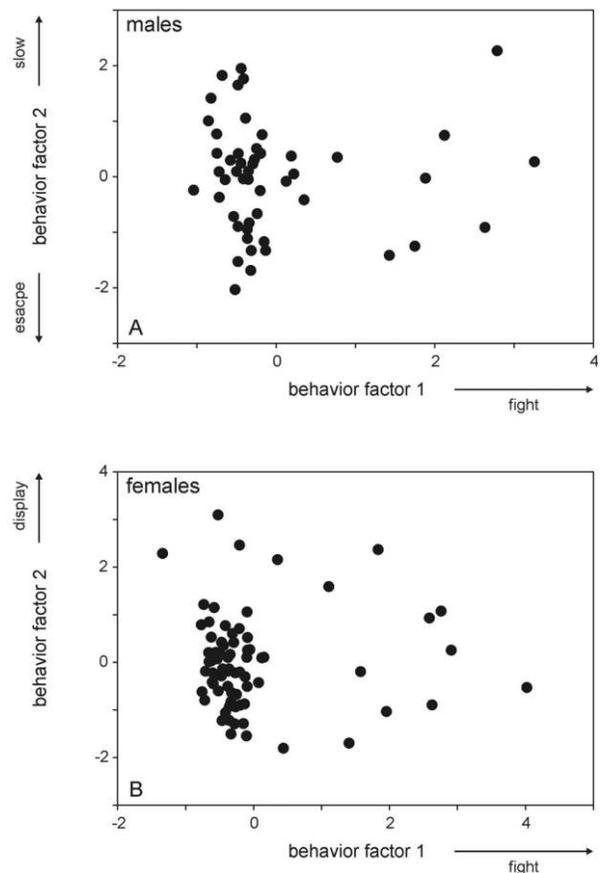


Figure 1. Scatterplots illustrating the results of a factor analysis performed on behavioral data for males (A) and females (B). The first factor is strongly correlated with the tendency for individuals to be aggressive in a situation where there is no escape possible, and it separates aggressive individuals from less aggressive ones for both males and females. The second factor for males is correlated with the propensity of an individual to try to escape (low scores) and the time needed to reach a shelter (high scores indicate that individuals took more time). For females, the second axis is correlated with aggressive behavior in an unfamiliar environment.

Table 1: Factor loadings of a factor analysis performed on the behavioral scores for male and female *Tupinambis merianae*

| Parameter | Male | | | Female | | |
|--------------------------|-------------|--------------|-------------|-------------|-------------|-------------|
| | Factor 1 | Factor 2 | Factor 3 | Factor 1 | Factor 2 | Factor 3 |
| Eigenvalues | 2.84 | 1.82 | 1.35 | 2.60 | 1.79 | 1.62 |
| Variance explained (%) | 31.51 | 20.22 | 15.03 | 28.86 | 19.88 | 17.99 |
| Response type familiar | .578 | .213 | .464 | .434 | .693 | .074 |
| Arching familiar | .156 | -.257 | .664 | .511 | .308 | .500 |
| Response type unfamiliar | .728 | .546 | -.024 | .137 | .824 | -.020 |
| Arching unfamiliar | -.032 | .017 | .797 | .465 | .325 | .377 |
| Time to shelter | .029 | .839 | -.043 | -.212 | .547 | -.564 |
| No. aggressive behaviors | .940 | .000 | .010 | .962 | .101 | -.004 |
| No. bites | .909 | -.027 | -.041 | .955 | .120 | -.010 |
| No. sprints | -.011 | -.839 | .100 | -.158 | -.300 | .773 |
| Response type tap test | .485 | -.053 | .219 | .062 | .124 | .552 |

Note. Bold indicates loadings >0.7. Factors are described in "Behavioral Analysis."

bite (4). All these scores were entered in a spread sheet and used as input for a factor analysis.

Bite Forces

In vivo bite forces were measured using an isometric Kistler force transducer (9311B; range, ± 5.000 N; Kistler, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (5995A; Kistler, Switzerland; see Herrel et al. 1999; Anderson et al. 2008 for a more detailed description of the setup). When the free end of the holder was placed between the jaws of an animal, prolonged and repeated biting resulted. The place of application of bite forces was standardized for all animals. Gape angle was standardized by moving the bite plates away from each other for larger animals. Measurements were repeated five times for each animal, and the maximum value obtained during such a recording session was considered to be the maximal bite force for that individual.

Analyses

Data were analyzed separately for males and females, because *Tupinambis merianae* is a strongly sexually dimorphic species and so patterns could be expected to be different for males and females. All behavioral scores were incorporated into a factor analysis with varimax rotation to reduce the dimensionality of the data set. Three factors were extracted, and factor scores were saved and used as new variables. Factor scores were correlated to \log_{10} -transformed bite force and \log_{10} -transformed snout-vent length (a proxy for body size) for males and females separately to test for associations between behavioral and performance traits. To test whether correlations between performance and behavioral scores were mediated by body size, residual bite forces were calculated from the regression of \log_{10} -transformed bite force on \log_{10} -transformed snout-vent length and correlated with the behavioral factors.

Results

Behavioral Analysis

The results of our behavioral analyses indicate distinct differences between individuals in their responses to a potential threat (Fig. 1). For males, the factor analysis retained three axes, together accounting for 66.76% of the variation in the data. The first factor, accounting for slightly over 30% of the variation, was positively correlated with the number of bites and the number of aggressive behaviors when placed in a confined space with no shelter (Table 1). Thus, individuals with high scores on this axis are generally aggressive. The second factor, accounting for about 20% of the variation in the data, was positively correlated with the time needed to reach a shelter and negatively correlated with the number of sprints in the confined space (Table 1). Thus, individuals scoring highly on this axis did not show a great tendency to escape, even when provided with the option of escape to a shelter. Finally, the third factor, accounting for another 15% of the variation, was positively associated with arching in an unfamiliar environment (Table 1). Thus, animals scoring highly on this axis tended to display this behavior.

For females, results were generally similar (Table 1; Fig. 1B). Again, the first factor was highly and positively correlated with the number of bites and the number of aggressive behaviors when placed in a confined space with no shelter. The second factor, however, differed from that for males and was positively correlated with the response type in an unfamiliar environment. Females scoring highly on this axis tended to show more aggressive behaviors when placed in an unfamiliar environment. The third factor was positively correlated with the number of sprints in a confined space, and females scoring highly on this axis showed a tendency to escape from aversive stimuli.

Interestingly, the responses of individuals in a familiar environment did not contribute strongly to the behavioral variation in the data set for both males and females, suggesting a more similar response across individuals. However, individuals

Table 2: Correlations between performance (bite force) and behavior for male and female *Tupinambis merianae*

| Sex, Parameter | Snout-Vent Length | Factor | | |
|----------------------|-------------------|--------|-------|--------|
| | | 1 | 2 | 3 |
| Male ($N = 50$): | | | | |
| Bite force | .966** | .365* | .424* | .060 |
| Snout-vent length | ... | .365* | .419* | .063 |
| Residual bite force | ... | -.023 | .076 | -.01 |
| Female ($N = 70$): | | | | |
| Bite force | .975** | .332* | .231 | -.412* |
| Snout-vent length | ... | .365* | .211 | -.416* |
| Residual bite force | ... | .046 | .077 | .006 |

Note. Entries are Pearson correlation coefficients. Factors are described in "Behavioral Analysis."

* $P = 0.05$.

** $P = 0.01$.

that were aggressive in both unfamiliar and confined spaces also tended to show greater aggressive scores in a familiar environment (Table 1).

Bite Force and Behavior

Our data indicate that bite force is significantly correlated with the behavioral factors retained from our behavioral analysis (Table 2). In males, bite force was significantly correlated with the first and second factors, indicating that animals with greater bite force were more aggressive in a confined environment (Fig. 2A) and were more reluctant to escape from a negative stimulus (Fig. 3A). For females, results were similar, and females with higher bite forces were also more aggressive in a confined environment (Fig. 2B) and more reluctant to escape (Fig. 3B). However, bite force was not correlated with the second axis in males, indicating that males with higher bite forces did not tend to display (i.e., arch) more often. Interestingly, in females, bite force was not associated with response type in an unfamiliar environment, even though this factor explained a considerable amount of the behavioral variation among females (Table 2).

Both the first and second behavioral factors were also positively correlated with body size in males (Table 2), suggesting that larger males were more aggressive, escaped less, and needed more time to reach a shelter. In females, body size was correlated with the first and third behavioral factors (Table 2). Thus, larger females were more aggressive and showed fewer escape behaviors.

Discussion

Our results show that there is a significant positive correlation between aggressive behavior and bite force and body size; large individuals with high bite force were more aggressive and showed fewer escape responses in an unfamiliar or restricted environment. Surprisingly, the behavioral responses of some individuals were different in different contexts. In their home enclosure, animals were generally less aggressive, and individ-

uals with high bite forces did not show significantly more aggressive behaviors. Individuals with high bite forces also did not tend to escape when in their home enclosure, suggesting that they were relatively unresponsive in general. However, the sequential decrease of the space available to the lizards in consecutive tests clearly evoked aggressive responses. Although it is unclear at this point why animals were generally reluctant to show aggression in their home enclosures, this may be related to the fact that lizards are used to humans because they are fed regularly, and consequently, they may not consider humans to be a severe potential threat when in a familiar environment. In an unfamiliar or restricted environment, however, animals with high bite forces were more inclined to show aggressive behaviors and would generally stand their ground and attack rather than run away from a potentially negative stimulus. Although display behavior (i.e., arching) was the main variable correlating with the third behavioral axis in males, this axis was not correlated to bite-force capacity. The presence or absence of arching during the behavioral responses of the lizards thus does not reflect their ability to bite.

The negative correlation between bite-force capacity and the number of sprints (i.e., escape bouts) observed in this study is

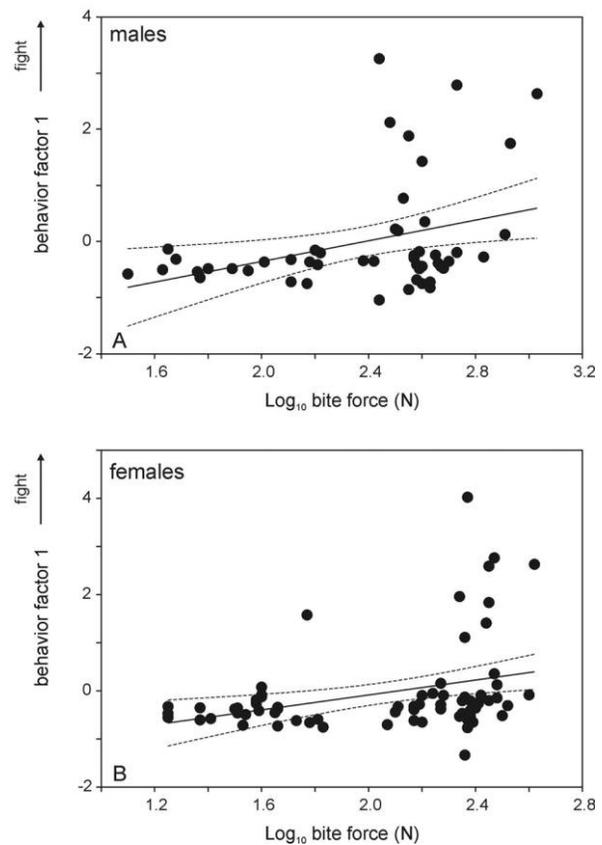


Figure 2. Scatterplot illustrating the relation between the tendency of an animal to fight when unable to hide and bite force in *Tupinambis merianae*. Although the relation is significant for both sexes, bite force is a much better predictor of behavior in males (A) than females (B). Dashed lines represent 95% confidence limits of the slope.

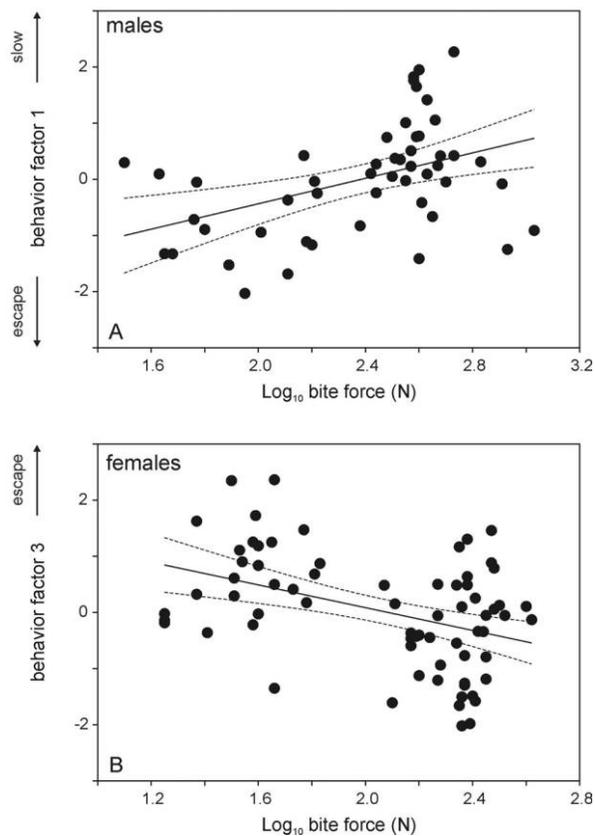


Figure 3. Scatterplot illustrating the relation between behavior and bite force in *Tupinambis meriana*. Males with higher bite forces take more time to reach their shelter and show a decreased tendency to escape (A). Females with higher bite forces also showed a decreased tendency to escape (B). Dashed lines represent 95% confidence limits of the slope.

suggestive of a fight versus flight trade-off. Such trade-offs have been documented in detail in mammals (Pasi and Carrier 2003; Kemp et al. 2005; Carrier 2007). In mammals such as dogs, for example, it has been demonstrated that the morphology of the locomotor system observed in individuals that are good fighters is incompatible with a morphology needed to run fast (Pasi and Carrier 2003; Kemp et al. 2005). Also, in *Tupinambis meriana* lizards, animals that were good biters took more time to reach their shelter and displayed fewer sprint bouts in a restricted environment. Given that lizards were all near their optimal body temperature during our behavioral trials, this observation is probably not the result of a temperature-dependent shift in behavior (Hertz et al. 1982; Herrel et al. 2007). Whereas this might suggest that a design for fighting (as characterized by large body size and a big head and jaw muscles) may detrimentally affect sprinting capacity, the greater time needed to reach a shelter might also be the consequence of behavioral reluctance to run rather than the result of an inability to run. Although this needs to be tested directly by measuring both sprint speed and bite-force capacity in the same individuals, it seems probable that the extremely large heads of in-

dividuals with large bite forces may actually negatively affect their ability to run fast.

Previous authors have suggested an important effect of body size in mediating the outcome of aggressive encounters between conspecifics (Chani 1995; Goldsmith et al. 1996; Nowbahari et al. 1999; Whiting et al. 2006; Hoyer et al. 2008). Indeed, because larger animals are bigger and have greater absolute levels of physical performance, they are presumably more likely to win an aggressive encounter. In our sample of *T. meriana*, bite force and aggressive behavior were also positively correlated with the overall size of the lizard (Table 2). Interestingly, the slope of the regression of bite force on snout-vent length was greater than the expected value of 2 (males: 2.75; females: 2.63; all else being equal, force should scale to linear dimensions with a slope of 2 because force is proportional to the cross-sectional area of the muscles), indicating that larger individuals are disproportionately better at biting. Thus, our data suggest that animals with large body sizes may be more aggressive because (1) they probably have a decreased risk of physical injury because of their large body sizes, and (2) they have disproportionately high bite forces, making them more likely to gain from engaging in aggressive encounters.

Although we do not know whether aggression in the individuals in our study was also mediated by higher circulating hormone levels, studies are currently underway to examine the proximate mechanisms underlying the variation in aggression and bite force in a subset of individuals. In summary, we suggest that, because bite force increased dramatically with body size, large body size and high bite force may reduce the threshold for an individual to engage in an aggressive encounter, allowing it to potentially gain or maintain resources and fight off predators while minimizing the risk of injury.

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