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RESEARCH PAPER

Sex, Age, and Population Density Affect Aggressive Behaviors in Island Lizards Promoting Cannibalism

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Abstract

Island populations may evolve distinct behavioral repertoires as a response to the conditions of insular life. Strong intraspecific competition is typical in insular lizards and may include cannibalism. In this study, we investigated sexual and age patterns of aggression in two populations of the Skyros wall lizard (*Podarcis gaigeae*), one from the main island of Skyros (Aegean Sea, Greece) and another from the satellite islet Diavates. The latter is terrestrial predator-free biotope, hosting a dense population of large-bodied lizards that have been reported to exert cannibalism. In staged encounters, we examined the aggressive propensities of adult male and female lizards against their age-peers and juveniles. Males from both populations were much more aggressive than females toward juveniles and other adults. Males from Diavates were more frequently aggressive to juveniles and other male lizards than males from Skyros. Diavates cannibals also captured their targets at shorter latency. We ascribe this distinct behavioral pattern to the high population density. Infanticide and intramale aggressiveness confer two great advantages to cannibals: food and elimination of future rivals.

Introduction

Island life deviates in many ways from mainland biological norms (MacArthur & Wilson 1967). The Island Syndrome (Adler & Levins 1994) and Island Rule (Van Valen 1973) describe some of the adaptations that animals have developed in response to insularity. In lizards, insular species and populations differ from their continental peers in a constellation of features such as body size, life history, digestion, thermal biology, and defense (Pafilis et al. 2007; Meiri et al. 2011; Novosolov & Meiri 2013; Sagonas et al. 2013a; Cooper et al. 2014). Behavior represents no exception. Particular behaviors have been described from insular populations, such as island tameness (Cooper et al. 2009a, 2014) and strong intraspecific competition (Pafilis et al. 2008; Vervust et al. 2009).

Islands host depauperate communities that experience lower predation risk and relaxed interspecific competition (Losos & Ricklefs 2009). As a result, insular populations of lizards are particularly dense (Rodda et al. 2001; Novosolov et al. 2013), triggering high intraspecific competition. This form of competition includes aggression that frequently causes amputation of body parts such as toes (Vervust et al. 2009) or tails (Jennings & Thompson 1999; Cooper et al. 2009b). The most severe expression of intraspecific competition is the killing and consumption of juvenile conspecifics (Jenssen et al. 1989; Elgar & Crespi 1992).

Filial cannibalism depends upon a range of ecological conditions and population-level resource competition (Klug et al. 2006; Bonsall & Klug 2011). The evolution of this strategy requires a trade-off between current and future reproductive success in which current loss is minimized by the consumption of lower-quality offspring (Manica 2004; Klug & Bonsall 2007). Furthermore, infanticide may have a strong impact on community structure and trigger shifts in juveniles' biology (Melton 1982; Wagner & Wise 1996; Keren-Rotem et al. 2006). Both sexes may engage in filial cannibalism (Bartlett 1987), only females (Klemme et al. 2006; females are more prone to sexual cannibalism, Pruitt et al. 2014) or, more frequently, only males (Mehlis et al. 2010). However, factors that lead to differences in infanticide among populations within a single species are poorly understood.

In this study, we aimed to shed light on the factors that promote cannibalism in small island communities. To this end, we assessed the cannibalistic behavior in different populations of the endemic Skyros wall lizard (*Podarcis gaigeae*; Aegean Sea, Greece). Twenty-one islets surround the main island of Skyros and one of them, Diavates, harbors a lizard population that differs from the others in color morph (Runemark et al. 2010), thermoregulation strategy (Sagonas et al. 2013b), reproductive performance (Pafilis et al. 2011), and ectoparasite load (Pafilis et al. 2013). The most striking difference although lies in body size: lizards from Diavates are 40% longer, and almost 300% heavier than those in other populations (Pafilis et al. 2009a). Previous studies, based on stomach content analysis, provided solid evidence of cannibalism in Diavates: adult male *P. gaigeae* consumed body parts (tails and feet) of conspecifics and even entire juveniles (Adamopoulou et al. 1999; Pafilis et al. 2009a). Namely, only a low 1.2% of Skyros stomachs contained conspecifics' parts while the equivalent percentage for Diavates was 21.42%. Although some of the special features of the particular Diavates population have been attributed to intense intraspecific competition (Pafilis et al. 2009a, 2011; Sagonas et al. 2013b), no direct evaluation of cannibalism has been made.

To quantify the extent of cannibalistic propensities, we staged encounters in the laboratory and focused on two populations, one from Diavates and another from Skyros. We formulated three hypotheses. First, we expected that assaults on juveniles would be more frequent by male lizards than females as males are larger and more frequently cannibalistic in interspecific studies. Second, we anticipated that Diavates lizards would attack juveniles more frequently than their Skyros kin because their larger size makes cannibalism easier. Third, we predicted that, due to the more intense intraspecific competition on Diavates, adult lizards would behave more aggressively toward their age-peers than those from Skyros.

Materials and Methods

Study System

The Skyros wall lizard is a small-bodied lacertid with snout-to-vent length (SVL) approximately 60 mm and body mass ca. 6.6 g. The species is endemic to the Skyros Archipelago, where it occurs in almost all habitats (Valakos et al. 2008). The reproductive period lasts from early Mar. until late Jul., and females lay one to three eggs, although clutch size in Diavates may reach five eggs (Pafilis et al. 2011). *Podarcis gaigeae* eats primarily terrestrial arthropods, mainly insects (Adamopoulou et al. 1999).

Our study focused on a population from the main island of Skyros (area 207 km^2, location Palamari, N 38°57′44″, E 24°30′26″) and the giant's population from the satellite islet Diavates (area 0.019 km^2, N 38°47′20″, E 24°30′47″). Diavates has several important ecological particularities. It is a terrestrial predator-free islet that also has minimal interspecific competition (Pafilis et al. 2009a, 2011). There is only one other terrestrial vertebrate there, the Kotschy's gecko (*Mediodactylus kotshyi*), which does not compete with lacertids for food or space (Valakos & Vlachopanos 1989). The vegetation is lush, composed of nitrophilous species, contrary to the typical phrygana and maquis vegetation of the other islets (Bohling et al. 2002; Snogerup & Snogerup 2004). This dense herbaceous vegetation is supported by marine subsidies that reach the islet through a thriving colony of the yellow-legged gull (*Larus michahellis*) (Pafilis et al. 2011). The increased primary productivity of Diavates leads to a richer invertebrate fauna (Pafilis et al. 2013) that fuels the densest population recorded in the eastern Mediterranean: 850 individuals per hectare (Palamari population harbors 185 lizards per hectare, Pafilis et al. 2009a).

In two consecutive field seasons (late Jun. 2012 and 2013), we captured by noose 175 lizards (68 males, 41 females and 7 juveniles from Skyros and 29 males, 25 females and 5 juveniles from Diavates). We aimed only for non-gravid females (tested for gravidity with palpation). Lizards were transferred to the facilities of the Biology Department at the University of Athens. Lizards were housed in glass terraria (20 × 25 × 15 cm) at a constant temperature (25°C) and controlled photoperiod (12 h light: 12 h dark). One incandescent heat lamp (60 W) in each terrarium provided 8 h of light per day and permitted basking. Lizards were fed mealworms three times weekly and had access to water *ad libitum*. Food was withheld from all animals for the 48 h preceding the experimental trials.

Behavioral Tests

We recorded lizard behavior in staged encounters that were held in an arena of 150 cm^2 with a digital camera (Canon FS200) that was hidden behind a folding screen. In each trial, we first released the lizard expected to attack (the larger individual, see Cooper & Stankowich 2010; hereafter called predator) in the arena. After 15 min, we released the second lizard (hereafter called prey–lizard) and started recording. Prior to each trial, lizards were allowed to thermoregulate for an hour in a specially designed terrarium (Van Damme et al. 1986). All trials were performed during the morning and lasted 30 min. Adult individuals were used in only one trial, whereas juveniles were used in 2–4 trials each. The terrarium was cleaned between trials.

We tested four types of pairs: adult males vs. adult males, adult females vs. adult females, adult males vs. juveniles, and adult females vs. juveniles. We did not measure the behavioral responses of males toward females as the experiment took place in the reproductive period, making courtship and copulation more probable than aggression.

We identified four aggressive behaviors by the predator: approach (moving slowly toward the prey–lizard without attacking), run (running toward the prey–lizard without attacking), attack (chasing the prey–lizard without capturing), and capture (capturing and biting the prey–lizard, usually on the tail or the base of the head). We classified the cases in which the predator demonstrated none of the four behaviors as no response. When the predator attacked the prey–lizard, we interfered and released it from predator's grasp while the 30 min recording period was interrupted (see Martín & Forsman 1999). Juveniles that were attacked were excluded from further experimental trials.

Statistical Analysis

To assess differences in behavioral frequencies between islands and ages or sexes for significance, we conducted Fisher's exact probability tests. Because frequencies of approach, run, attack, and capture were often low, we pooled the frequencies of different behaviors in two ways. First, we computed the number of individuals that performed one or more of the behaviors approach, run, attack, and capture. Second, we computed the number of individuals that performed one or both of the two most aggressive behaviors, attack, and capture. Then, we used the statistical tests to compare frequencies of lizards that did and did not perform the behaviors.

Differences in latency to attack and body length were tested for significance using analysis of variance for two independent groups. Prior to analyses of variance, the assumptions of normality and homogeneity of variance were evaluated using Kolmogorov–Smirnov and Levene's tests, respectively. When variances were significantly heterogeneous, they were made homogeneous by logarithmic transformation. We used Pearson's correlation to assess the relationship between latency to capture and body size (SVL, measured using a digital caliper, Silverline 380244, accurate to 0.01 mm) difference between adult males and juveniles. We employed analysis of variance to compare populations in the body size difference between adult males and juveniles.

All tests were two-tailed with $\alpha = 0.05$. Latency to capture is reported as $\bar{x} \pm 1.0$ SE. Effect sizes are reported as $r_{\text{equivalent}}$ (Rosenthal & Rubin 2003) for Fisher's exact probability tests and as η^2 for analysis of variance (Cohen 1973). The former may be interpreted as a Pearson's product-moment correlation coefficient, and the latter is analogous to r^2.

Results

Males Vs. Juveniles

A significantly higher proportion of Diavates males (92%, 12 of 13) than Skyros males (42%, 15 of 26) performed one or more of the behaviors approach, run, attack, and capture (Fisher, $p = 0.0025$) (Fig. 1). This difference was even greater for the two most aggressive behaviors, attack, and capture: Males from Diavates (69%, 9 of 13) were significantly more likely than males from Skyros (17%, 6 of 36) to attack or capture juveniles (Fisher, $p = 0.0010$) (Table 2).

Among males that captured juveniles, latency to capture was far shorter for males from Diavates (133.0 ± 54.05 s, n = 5) than Skyros (787.5 ± 278.53 s, n = 3) (Table 1). Variances were significantly heterogeneous using the raw data (Levene's

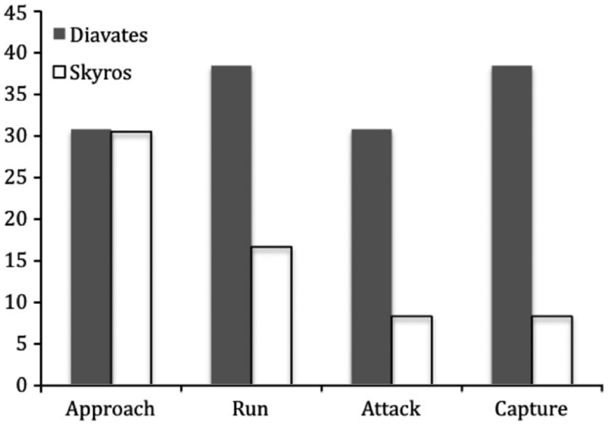

Fig. 1: Rates of male aggressive behaviors toward juveniles.

Table 1: Time between the insertion of juvenile and capture by male predator (in seconds)

Location	$\bar{x}$ ± SD (Range)	N	Mean ± SD (Range)	N
Diavates	133.00 ± 154.05 (36–406)	5	4.49 ± 0.92 (3.58–6.00)	5
Palamari	787.67 ± 278.53 (268–1802)	3	6.26 ± 1.08 (5.59–7.50)	3

$F_{1,6} = 17.47$, $p = 0.0058$), but were homogeneous for logarithmically transformed data (Levene's $F_{1,6} = 0.27$, $p = 0.62$). Using the transformed data, latency to capture was significantly shorter for males from Diavates than Skyros ($F_{1,6} = 6.18$, $p = 0.047$). Although the p value was barely significant due to small sample size, the effect size was large (Table 2). Latency to capture was not significantly correlated with the difference in SVL between adult males and juveniles ($F_{1,6} = 1.96$, $p = 0.21$), (Table 2). For all males, including those that did not capture juveniles, the difference in SVL between the adult and juvenile was significantly greater ($F_{1,47} = 117.27$, $p < 1 \times 10^{-6}$) for pairs of lizards from Diavates (72.4 ± 4.8 mm) than Skyros (56.3 ± 4.6 mm). Variances were homogeneous (Levene's $F_{1,47} = 0.12$, $p = 0.73$) (Table 2).

Male lizards from Diavates (832 ± 7 mm) were 1.36 times larger than those from Skyros (613 ± 7 mm). Variances of SVL were homogeneous (Levene's $F_{1,47} = 0.09$, $p = 0.77$), and lizards from Diavates were significantly longer than those from Skyros ($F_{1,47} = 240.45$, $p < 1.0 \times 10^{-6}$) (Table 2).

Males Vs. Males and Comparisons Between Interactions of Males Vs. Juveniles and Other Males

The proportions of focal males that performed one or more of the behaviors approach, run, attack, and capture did not differ significantly between males from Diavates (88%, 7 of 8) and Skyros (62%, 10 of 16) (Fisher, $p = 0.35$). However, males from Diavates were significantly more likely to perform the most aggressive behaviors, that is, attack or capture, (75%, 6 of 8) than were males from Skyros (12%, 2 of 16) (Fisher, $p = 0.0047$) (Table 2). Four Diavates males captured other males; none from Skyros did (Fig. 2).

Frequencies of aggressive behaviors by focal males directed to juveniles and other males were similar. The proportion of males that performed one or more of the behaviors approach, run, attack, or capture did not differ significantly between juveniles (55%, 27 of 49) and adult males (71%, 17 of 24) (Fisher $p = 0.22$). Neither did the proportion of focal males that attacked nor captured other lizards differ significantly between juveniles (31%, 15 of 49) and adult males (33%, 8 of 24) (Fisher, $p = 1.00$).

Table 2: Effect sizes for the focal behavioral traits

Trait	Effect size
Attack or capture (male vs. juvenile)	$r_{\text{equivalent}} = 0.43$
Any aggressive behavior (male vs. juvenile)	$r_{\text{equivalent}} = 0.40$
Latency to capture (male vs. juvenile)	$\eta^2 = 0.51$
Latency to capture in correlation with SVL	$r = -0.51$
Variances of SVL between males and juveniles	$\eta^2 = 0.71$
Variances of SVL between males	$\eta^2 = 0.84$
Attack or capture (male vs. male)	$r_{\text{equivalent}} = 0.52$
Variances of latency to attack (male vs. male; male vs. juvenile)	$\eta^2 = 0.60$
Attack or capture (male vs. juvenile; female vs. juvenile)	$r_{\text{equivalent}} = 0.38$
Any aggressive behavior (male vs. juvenile; female vs. juvenile)	$r_{\text{equivalent}} = 0.41$

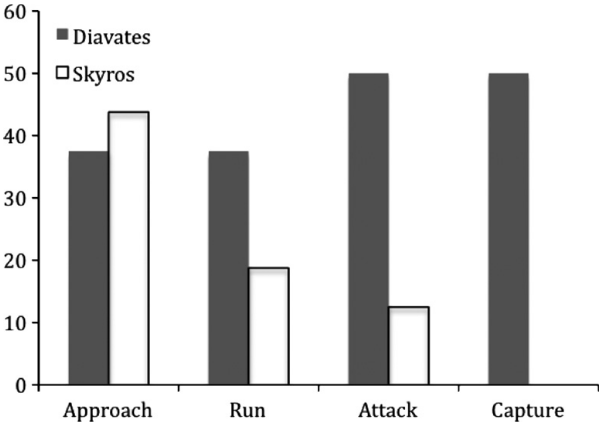

Fig. 2: Rates of aggressive behaviors between males.

Although frequencies of attacks and captures did not differ between juveniles and adult males, latencies to attack by focal males from Diavates were much shorter for juveniles (133.0 ± 68.9, n = 5) than adult males (542.5 ± 113.4 s, n = 4). Variances of latency to attack were homogeneous (Levene's $F_{1,7} = 2.24$, $p = 0.18$), and the difference was significant ($F_{1,7} = 10.46$, $p = 0.014$) (Table 2).

Females with Juveniles and Other Females Plus Intersexual Comparisons

Females were remarkably unaggressive. No females attacked or captured juveniles (0.0%, 0 of 30), and few performed either of the less aggressive approaches or runs (27%, 8 of 30) (Fig. 3). The difference in frequency of the less aggressive behaviors between Diavates (27%, 3 of 11) and Skyros (28.57%, 6 of 21) females was not significant (Fisher $p = 1.0$). Similarly,

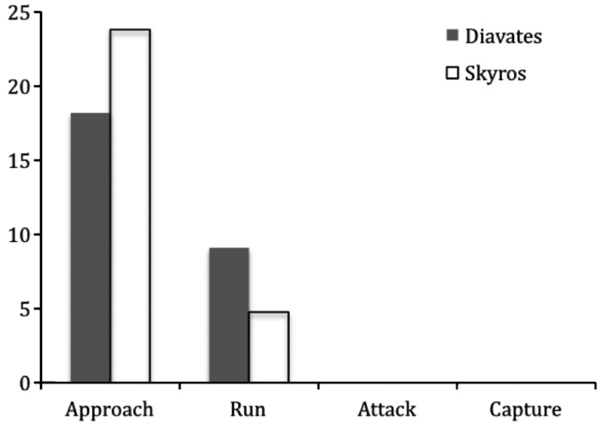

Fig. 3: Rates of female aggressive behaviors against juveniles.

no focal female attacked or captured an adult female (0.0%, 0 of 17), and only few performed the less aggressive behaviors (29%, 5 of 17) (Fig. 4). The difference in proportion of females that either approached or ran toward non-focal females between Diavates females (29%, 2 of 7) and Skyros females (30%, 3 of 10) was not significant (Fisher, p = 1.00).

Males were much more aggressive than females toward juveniles. Using data for lizards from both islands pooled, males performed one or more of approach, run, attack, and capture directed toward juveniles significantly more frequently than did females (males: 55%, 27 of 49; females: 27%, 8 of 30) (Fisher p < 0.0001). Males also attacked or captured juveniles (31%; 15 of 9) significantly more frequently than did females (0.0%, 0 of 30) (Fisher, p = 0.0003) (Table 2).

Discussion

Our findings support the three hypotheses we posed. Large male lizards from Diavates were far more aggressive to juveniles and other adult males than males from Skyros. Females were less aggressive than males. Furthermore, Diavates giants captured and attacked their targets at shorter latency compared with lizards from Skyros.

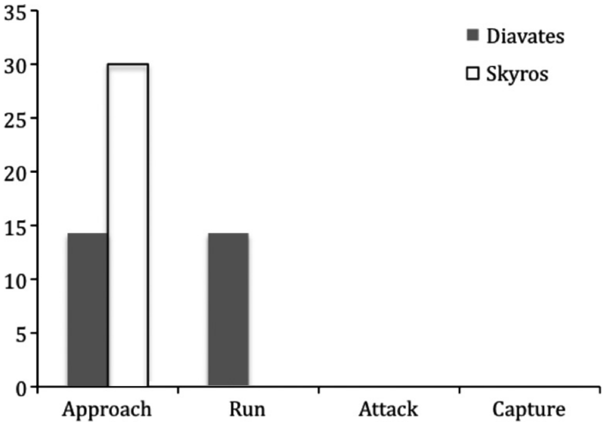

Fig. 4: Rates of aggressive behaviors between females.

Responses By Males to Juveniles and Adult Males

Males from Diavates pursued and attacked juveniles at much higher frequency than the Skyros males (Fig. 1) and attacked and captured juveniles at shorter latency (Table 1). These differences suggest that males from Diavates may have had previous experience as cannibals. Although latency to capture was not significantly correlated with the size difference, Diavates males attacked and captured juveniles much faster compared with their Skyros peers.

The larger size difference between pairs of lizards from Diavates than Skyros suggests that the relatively larger size of adult lizards from Diavates may facilitate cannibalism. Filial cannibalism is common among many taxa (Wagner & Wise 1996; Lourdais et al. 2005; Fowler & Hohmann 2010). Young offspring represent easy targets due to their smaller size and poorer locomotor performance (Polis 1981; Polis & Myers 1985; Martín & López 2003). Furthermore, infanticide is rather common in small islet lizard populations (Castilla 1995; Castilla & Van Damme 1996; Dappen 2011).

The underlying cause of cannibalism on islets may be related to their ecological features, particularly food scarcity and high population density. Cannibalism has been associated with low food abundance (Hoelzer 1992; Kvarnemo et al. 1998). Arid Mediterranean islets are characterized by limited food availability (Fuentes 1984; Brown & Pérez-Mellado 1994). To survive, island lizards often shift their diets from insectivory to omnivory (Van Damme 1999; Cooper & Vitt 2002; Herrel et al. 2004) and cannibalism (Pérez-Mellado & Corti 1993). Limited food resources are known to trigger cannibalistic propensities even in mainland populations (Amat et al. 2008). However, the food supply on Diavates does not conform to this general rule. The breeding colony of seagulls (*L. michahellis*) subsidizes the islet community with sea-derived energy in the forms of guano, fish scraps, and decomposing carcasses (Pafilis et al. 2011). As a result, food is abundant and suffices to support a very dense lizard population (Pafilis et al. 2013).

Lizard populations on islands often are much denser than on mainland (Buckley & Jetz 2007), and this applies to Mediterranean islets as well (Castilla &

Bauwens 1991; Pérez-Mellado et al. 2008). Dense populations suffer from overexploitation of energy resources and territories, leading to greatly increased intraspecific competition (Knell 2009; Calsbeek & Cox 2010). Adults competing for limited food and space may resort to filial cannibalism (Polis 1981; Jenssen et al. 1989). Infanticide confers many advantages to the cannibals: elimination of future antagonists, relaxation of intraspecific competition, and an excellent source of nutrients (Sargent 1992; Thomas & Manica 2003). In the overpopulated Diavates, food may be not in short supply in an absolute sense, but the pressure of intraspecific competition remains high. Consumption of juveniles may be naturally selected because it effectively reduces competition by eliminating future rivals for food and females. By obtaining nutritious meals from juveniles, cannibalistic males also reduce competition by decreasing population size and possibly by regulating population density if the rate of cannibalism is density-dependent.

Cannibalism on small Mediterranean islets is associated with high population density, including high juvenile density, in an otherwise food-limited environment. It remains to be determined whether the cannibals can recognize their own offspring. However, some lizards respond differentially to chemical cues from related and unrelated individuals (Martín & López 2006; Martín et al. 2007). In the Australian skinks *Egernia stokesii* and *Tiliqua rugosa*, mothers responded more strongly to chemical cues of their own offspring than those of unrelated young (Main & Bull 1996). Because some lizards are capable of individual recognition and other sophisticated discriminations using chemical senses (Mason 1992), pheromones may allow males to avoid cannibalizing their own offspring. This possibility requires experimental investigation.

Males from Diavates interacted more aggressively with other adult males than did Skyros males (Fig. 2). Males from the main island approached, ran toward and pursued other males, but, at lower frequency than Diavates males. They never captured other males (Fig. 2), whereas half of Diavates males captured other males. High lizard density may be the underlying reason for the strong aggressiveness by Diavates males. High population density is a major factor that increases the intensity of intrasexual competition (Emlen & Oring 1977; Knell 2009). In dense populations, agonistic encounters increase dramatically and intramale competition peaks (Mougeot et al. 2003; Kokko & Rankin 2006). The dense Diavates population favors aggressive responses.

Interestingly, in all cases of male–male interactions in the Diavates population, giant males aimed for the tail of the prey–lizard. The rates of regenerated tails have been traditionally considered as an index of predation pressure (Pianka 1970; Turner et al. 1982; Pafilis et al. 2009b). However, lizards may also shed their tails as a consequence of intraspecific aggression (Langkilde & Shine 2007; Pafilis et al. 2008). Field observations are in accordance with our findings. Although the rate of regenerated tails was only 32.16% in Skyros, the equivalent value for Diavates was 88.4% (Pafilis et al. 2009a).

The high rates of tail loss and regeneration of the Diavates population are impressive, given that no predators or interspecific competitors occur on the islet (Pafilis et al. 2011). Pafilis et al. (2009a) attributed these high rates to intraspecific competition, which highlights the tail as an ‘Achilles’ heel’ (Jennings & Thompson 1999) that attracts conspecific attacks. Our results verified this hypothesis. Many lizards store fat in their tails, at least seasonally (Vitt & Cooper 1986; Wilson 1992; Roig et al. 2000) and *P. gaigeae* likewise store lipids in caudal tissues (Pafilis et al. 2005). By attacking their conspecifics’ tails, giant males repel their rivals, may reduce their subsequent ability to mate (Fox & Rostker 1982), and gain an energetically rich meal.

Lethal cannibalism on juveniles and non-lethal cannibalism on adults, that is, energetically and socially costly to the victimized individuals may enhance the fitness of cannibalistic males by providing extra nutrition (although it is not food scarcity that triggers cannibalism in the rich, in terms of resources, Diavates) and by reducing the competitive ability of males that have lost tails as sexual competitors. Because larger males may be better able to capture and subdue conspecifics, natural selections should favor large body size when benefits of cannibalism outweigh costs such as consumption of relatives and elimination of potential future mates from the population.

These considerations may explain why cannibalism seems to lead to larger body size, even gigantism (Howard et al. 1998; Claessen et al. 2000; Calsbeek & Smith 2007). Infanticide exerts a strong selective pressure for larger offspring as large size renders important advantages (e.g. better physiological performance and predation avoidance) for survival in dense populations (Case 1978; Meiri 2008) in addition to the ability to cannibalize conspecifics upon reaching adulthood. The combined effects of food availability and cannibalism seem adequate to account for the presence of gigantism in Diavates.

Female Responses and Comparison Between Sexes

Females from both populations rarely exhibited any potentially aggressive responses to juveniles, and no females attacked or captured juveniles (Fig. 3). These results corroborate a previous report that all *P. gaigeae* that had consumed body parts of conspecifics were males (Adamopoulou et al. 1999). Female *Podarcis* lizards have been reported to show lower cannibalistic propensities in western Mediterranean islets as well (Castilla & Van Damme 1996; Carretero et al. 2010). This sex difference in tendency to cannibalism is presumably, at least partially, attributable to the shorter SVL of females. Their smaller body size precludes them from consuming an entire juvenile. Another possible explanation could be the smaller head and lower bite force of females, a common feature in lacertids (Herrel et al. 1996, 1999, 2001; Sagonas et al. 2014). However, our experiment was designed to assess only cannibalism by infanticide or tail consumption. Another case of cannibalism is oophagy (Elgar & Crespi 1992). Consumption of eggs by females is common in reptiles (Huang 2008; Mociño-Deloya et al. 2009). Female *P. gaigeae* might eat eggs of conspecifics, but we have no direct evidence that they do. Nevertheless, some degree of oophagy is likely as this practice occurs in other insular *Podarcis* lizards (Dappen 2011; Brock et al. 2014).

Very few aggressive behaviors were recorded between females (Fig. 4), and these were limited to approaches and a few runs, the latter only by Diavates females. Although males use aggressive behavior for intrasexual competition for space and mate control, females do not defend territories (Braña 1996; Moreira et al. 2006). Furthermore, because some male lizards aggressively maintain harems (Zamudio & Sinervo 2000), females may interact frequently with other conspecifics females within a restricted area (although harems are rather unlikely in the case of insular lacertids).

As expected, the frequency of aggressive responses between males from both populations was much higher than that between females. The high percentages of aggressive behavior between males reflect their intrasexual competition for territory, food, and mates (Yasui 1998; Lailvaux & Irschick 2007; McEvoy et al. 2012). Intrasexual competition in male lizards often leads to fighting, which may inflict injury because the larger heads of males exert high bite force (Cooper & Vitt 1987; Husak et al. 2009; Herrel et al. 2010). Weaker intrasexual competition and inability to exert such high bite forces may limit the motivation of females for aggression and ability to be cannibals.

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