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The relationship between perch type and aggressive behavior in the lizard *Norops polylepis* (Squamata: Dactyloidae)

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Abstract

The relationship between perch type and aggressive behavior in the lizard *Norops polylepis* (Squamata: Dactyloidae). The intensity of aggression against intruders by owners of a territory has been related to the type of resources available to an individual within its territory. The influence of perch-site characteristics on aggressive behavior of resident male *Norops polylepis* in presence of an intruder male was investigated in this study. At each perch site, pairwise encounters were conducted in which the aggressive behavior of resident males was recorded, along with the diameter of the perch and the number of nearby perches. Aggressive behavior of resident males increased on larger perches and to some extent in areas having greater density of nearby saplings. Potential explanations for the high aggressive behavior of *N. polylepis* on broad perches with high number of neighboring saplings are explored.

Keywords: aggression, agonistic behavior, anoles, intruder, perching site.

Resumen

Relación entre el tipo de percha y el comportamiento de agresividad en el lagarto *Norops polylepis* (Squamata: Dactyloidae). La intensidad de agresión por individuos que son dueños de un territorio hacia los intrusos se ha relacionado con el tipo de recurso disponible en sus territorios. La influencia de las características del sitio de percha con el comportamiento de agresividad de los machos residentes de *Norops polylepis* en presencia de un macho intruso se investigó en este estudio. En cada sitio de percha se registró el comportamiento agresivo de los residentes, junto con los diámetros de percha y árboles jóvenes alrededor. Se encontró evidencia de que la agresión de los residentes incrementó en perchas con mayor diámetro y áreas con mayor densidad de árboles jóvenes. Explicaciones potenciales por el alto nivel de agresividad de *N. polylepis* en perchas anchas y con mayor número de árboles jóvenes alrededor fueron exploradas.

Palabras Clave: agresividad, anoles, comportamiento agonístico, intruso, sitio de percha.

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Resumo

Relação entre tipo de poleiro e comportamento agressivo no lagarto *Norops polylepis* (Squamata: Dactyloidae). A intensidade da agressão contra intrusos por detentores de um território tem sido relacionada ao tipo de recurso disponível para um indivíduo no interior de seu território. A influência das características do poleiro sobre o comportamento de agressão de machos residentes de *Norops polylepis* na presença de um macho intruso foi investigada neste estudo. Em cada poleiro, foram conduzidos encontros nos quais foi registrado o comportamento agressivo dos machos residentes, além do diâmetro do poleiro e o número de poleiros das proximidades. O comportamento agressivo de machos residentes aumentou em poleiros maiores e em algum grau em áreas com maior densidade de plântulas ao redor. São discutidas explicações potenciais para o alto grau de comportamento de agressão de *N. polylepis* em poleiros grandes e com elevado número de plântulas ao redor.

Palavras-chave: agressão, comportamento agonístico, intruso, local de empoleiroamento.

Introduction

Aggressive or agonistic behavior has been studied in a broad range of animal taxa for decades (Maher and Lott 1995, Calsbeek and Sinervo 2002). Aggressive behavior has been related to the consistent use of a particular area (Sheldahl and Martins 2000), often among males (Archer 1988), and may manifest in different forms—e.g., advertisements (e.g., visual displays) to physical contact (Martins 1994, Moore 2007). Typically, agonistic interactions between conspecifics are resolved through the use of non-physical communication that precedes physical contact. However, in some circumstances, agonistic behavior results in combat between rival individuals; this behavior can be costly for individuals, because resulting physical injury may significantly affect the individual fitness (Riechert 1998). Agonistic behavior also can be costly to territory owners that employ energetically expensive actions to exclude intruders (Burghardt 1988, Camfield 2006).

The intensity of aggression by territory owners against intruders may vary in accordance with available resources in the habitat (e.g., retreat sites from predators, food, females etc.; Leuck 1995, Bradbury and Vehrencamp 1998, Calsbeek and Marnocha 2006). Previous studies of *Norops sagrei* revealed that aggression of residents against intruders differed between ground and elevated perch sites within territories; this suggests that both perch sites are important to anoles in differing ways (Calsbeek and Marnocha 2006). For example, elevated perching sites may provide better scanning sites to protect valuable areas on the ground (Baird and Sloan 2003).

Anoles are important models for understanding factors that influence aggressive behavior because they exhibit intraspecific aggression by defending specific sites (e.g., basking sites) and/or home ranges (McMann and Paterson 2012). Aggressive behavior in anoles involves a variety of visual displays, such as headbobs, push-ups, dewlap extensions, and lateral body compression that can advance to physical contact (Jenssen 1977, McMann 2000, Paterson 2002, Perry *et al*. 2004). These defensive behavioral patterns might vary during encounters, and level of aggression in anoles has been related to the type and frequency that these patterns are conducted during such events (Hurd 2004, Simon 2011, McMann and Paterson 2012).

Previous studies have suggested that anoles such as *Norops polylepis* (Peters, 1874) use perches as refuges from predators (Stamps 1987), and larger-diameter perches may facilitate sprint speed to obtain food or escape from predators (Losos *et al*. 1997, 2000), increase predator avoidance, and improve detection of approaching predators (Scott Jr. *et al*. 1976). In addition, increased structural complexity may provide more foraging and refuge sites (Hertz 1974). Therefore, if perches are resources valued by individuals, we might expect that larger perches located near foraging and/or refuge sites might be more important for males to defend.

We examine variation of agonistic behavior of resident male *Norops polylepis* in presence of an intruder male relative to the characteristics of their perching sites. We hypothesized that magnitude of aggressive behavior of resident males is influenced by the perch diameter and structural complexity (e.g., number of saplings) around their perching site, and predicted that resident males would be more aggressive to intruder males in the defense of large perches surrounded by complex vegetation.

Materials and Methods

Study Site

This study was conducted in a secondary growth rainforest at Piro Biological Station at the Osa Conservation Area in Osa Península, Costa Rica (08º24'16.2" N, 83º20'14.7" W). The habitat at the study site possessed a semi-closed canopy with relatively sparse understory vegetation in July 2012 and December 2013, during the rainy and dry seasons, respectively, when this study was conducted.

Study Species

Norops polylepis is a Central American lizard that is a common inhabitant of the shady understory of rainforests in southwestern Costa Rica and western Panama (Hertz 1974, Janzen 1991). Males are territorial and spend approximately half of their time displaying or fighting with other males (Andrews 1971). Males usually perch up to 2 m above the ground on saplings surrounded by shrubby and herbaceous vegetation (Barquero and Arguedas 2009, Cortés-Suárez and Díaz-Gutiérrez 2013), with perch heights differing in the rainy and dry seasons (Andrews 1971). Individuals typically perch head-down on a vertical surface to survey for food and remain alert to social interactions and predators (Scott Jr. *et al*. 1976). The species often postures with the head directed downward on tree trunks, a posture that is common in anoles of the trunk-ground ecomode of the Caribbean.

Observations of Aggressive Behavior

To assess aggressive behavior in adult male *Norops polylepis,* we conducted 41 focal observations of territorial residents in the presence of a male intruder. Observations were conducted in the morning (09:00–12:00 h) and afternoon (13:00–16:00 h). For each experimental observation, we first captured an adult male *N. polylepis* by hand to use as intruder and measured its snout–vent length (SVL; ±1 mm) with calipers. Then, we searched for a resident male perching head downward on a sapling trunk. Because male *Norops* exhibit neighbor recognition and respond with greater aggression during territory defense with unfamiliar males (McMann and Paterson 2003, 2012), we selected resident males >100 m away from the intruder male's perch to avoid any confounding effects with neighbor recognition. Once we found a resident male meeting that criterion, we attached the intruder to a thin, 1 m long wooden pole by tethering it around the waist with a 1.3-m brown silk thread. We then gently placed the tethered intruder about 20 cm away from the resident male and recorded the types and iterations of aggressive behavior by the focal male during a 4-min period. Resident males appeared oblivious to the motionless observer about 1 m away (Andrews 1971); thus, our presence likely did not cause any disturbances. After the observation period was finished the intruder was released at its capture point, and the focal male was captured to measure its SVL and characterize its perch site (described below).

The agonistic behaviors were measured following the protocol of Perry *et al*. (2004) and Calsbeek and Marnocha (2006) and included the following: dew-lapping (full or partial extension of colorful dewlap); push-ups (body movements up and down in a vertical plane, performed by flexion and extension of the forelimbs); dewlap bouts (dewlap extension performed at the same time with push-ups); lateral display (lateral body compression with dewlap extension); attack (any physical contact, e.g., bites); and retreat. Attacks were brief and did not result in physical injuries. None of the intruders performed any aggressive behavior toward the resident. Our scoring index to determine the degree of aggression of focal males followed those of Perry *et al*. (2004), Calsbeek and Marnocha (2006), and Lailvaux *et al*. (2012). Dewlap extension, push-ups, and dewlap bouts were assigned a value of 0.5; lateral displays were valued as 1 and retreats were as -1. An overall score was assigned to each resident male by summing the values from all the observed behaviors that were observed and recorded during observations.

We measured the perch diameter (cm) of each resident's perch with a diameter tape, and counted the saplings surrounding the perch site in a 4 × 4 m quadrant centered on the perch site. A sapling was defined as an immature tree with a slender trunk and height ranging from 1 to 3 m. Before releasing males, we marked them with paint to avoid using individuals more than once within either study period.

Statistical Analysis

Because large differences in body sizes between resident and intruding lizards might influence agonistic interactions, we examined whether significant differences existed (Chellappa *et al*. 1999, Johnsson *et al*. 1999, Calsbeek and Sinervo 2002, Aragón *et al*. 2006). In the first analysis, a linear model hypothesizing an effect of residential status (resident/intruder) and a null model (no effect of residential status; hypothesizes a difference of 0) were constructed; SVL was the response variable. Then, we conducted model-averaged effect sizes; this is an information-theoretical alternative for comparisons between groups and is useful when the focus is to determine the effect of a given factor (Mazerolle 2014). This model-averaged computes the unconditional standard error and unconditional confidence intervals as described in Burnham and Anderson (2002).

To assess the relationship between aggression and perch type of resident males in the second analysis, we formulated a candidate set of linear models with the aggression score as the response variable. Perch diameter and number of saplings were predictor variables, and a model with an additive effect with both predictors was included because we were concerned that these variables could have synergistic effects. The data were log-transformed to improve normality. We did not detect multicollinearity using variance inflation factors (VIF < 2 in the global model; Kutner *et al*. 2004); thus, both predictors were included in our analyses. We used Akaike Information Criterion adjusted for small sample sizes (AICc) to rank our models (Burnham and Anderson 2002). We also used AICc weight (w) and ΔAICc value (Burnham and Anderson 2002). As a result of the model selection uncertainty from the candidate models of the second analysis, no model had $w > 0.90$, we conducted model averaging (Symonds and Moussalli 2011). The model averaging produces parameter estimates and standard errors that take into account within-model uncertainty and additional uncertainty about which model best characterizes the true biological process being tested (Burnham and Anderson 2002, Ruiz-Gutiérrez *et al.* 2008); these multi-model inference procedures reduce bias and increase precision (Symonds and Moussalli 2011). We also summed the AICc weights (w) in which a specific predictor was included in a model to rank it in terms of importance. This provides a more robust assessment of variable importance, relative to single-model approaches (Burnham and Anderson 2002).

All analyses were conducted in R version 3.1.2 (R Development Core Team 2014) using the package "AICcmodavg" (Mazerolle 2014) to calculate AICc and model-averaged effect sizes, and the package "MuMIn" (Bartoń 2014) to compute model-averaged estimates and predictions. Means are given ±1 SE.

Results

The model selection process identified the model without any effect of residential status as the most well supported model given the data (Table 1), and unconditional confidence intervals from model averaged broadly overlapped zero (95% C.I. = -0.76 – 0.84). Therefore, these models indicate that there is no difference of body size (model average effect size = 0.04, unconditional SE = 0.41) between resident (49.9 ± 0.37 mm) and intruder males (49.8 ± 0.35 mm).

Perch diameter ranges from 1.0–13.0 cm (3.5 ± 0.4), and the number of saplings from 7–27 (13.0 ± 0.8). The model consisting of only perch diameter was the best supported model, but it was followed closely by the global model (ΔAICc = 0.82, Table 2). Therefore, model-averaged estimates (Table 3) and predictions indicate that residents have a higher aggression score as perch diameter increases (Figure 1A) and the number of neighboring saplings has a weak positive relationship with aggression score (Figure 1B). The relative importance of perch diameter and number of saplings are 1.00 and 0.40, respectively.

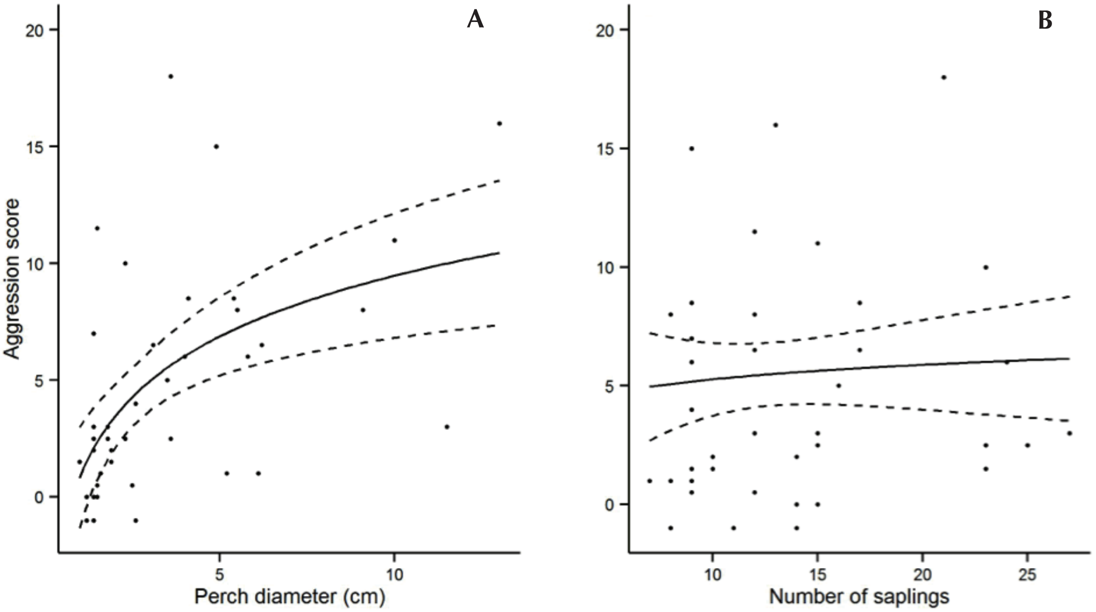

Figure 1. Effect of (**A**) perch diameter and (**B**) number of saplings around perching site with aggression score of male *N. polylepis* residents against intruders during 4-min trials. The continuous lines indicate the predicted fit from the averaged predictions and dashed lines are 95% confidence intervals. Circles indicate observations.

Table 1. Candidate set of linear models describing how body size differ between intruder and resident males. Number of parameters (*K*), Akaike's Information Criterion values (AICc), difference in AICc between the current and the best model (ΔAICc) and AICc weights (*w*). The null model of no difference in body size between intruder and residential males was most highly supported.

Model	*K*	AICc	ΔAICc	*w*
Null model	2	333.7	0.0	0.74
Residential status	3	335.8	2.1	0.26

Table 2. Candidate set of linear models for degree of aggression of resident males against intruders to log perch diameter and log number of saplings surrounding the perching site. Number of parameters (*K*), Akaike's Information Criterion values (AICc), difference in AICc between the current and the best model (ΔAICc) and AICc weights (*w*).

Model	*K*	AICc	ΔAICc	*w*
Log perch diameter	3	235.80	0.00	0.60
Log perch diameter + Log saplings	4	236.63	0.82	0.40
Null model	2	248.42	12.62	0.00
Log saplings	3	250.10	14.29	0.00

Table 3. Model-averaged estimates for log perch diameter and log number of saplings surrounding the perching site that predicts aggression score of resident males against intruders. Standard error (SE).

Parameter	Regression estimate	SE	Adjusted SE
Intercept	-1.47	4.17	4.25
Log perch diameter	3.75	0.91	0.94
Log saplings	0.88	1.55	1.58

Discussion

The aggression intensity of resident male *Norops polylepis* toward intruders is correlated with the perching sites of the residents. It is positively correlated with perch size and to some extent with density of nearby saplings. Wider-diameter perches may defended more vigorously because they provide retreat sites that maximize the probability of detecting approaching predators and improve predator avoidance (Scott Jr. *et al*. 1976, Stamps 1987). The main predators of *N. polylepis* are birds (e.g., trogons) with acute color vision and shape recognition (Stamps and Gon 1983, Savage 2002). Therefore, males that expose their conspicuous dewlaps during social interactions may also be at great risk of predation on perches with smaller diameter. This is important because *N. polylepis* lives in an environment where predation pressure is high (Andrews 1979). Also, because male *N. polylepis* spend about half of their time engaged in social behavior involving agonistic interactions, predator avoidance seems to be a primary evolutionary driver of behavioral patterns (Andrews 1971, Scott Jr. *et al*. 1976, Perry 1996). Broader perches may be defended more than narrower perches because the larger perches facilitate greater sprint speed when males are hunting prey or escaping predators (Losos *et al*. 1997, 2000); however, this hypothesis must be tested by research on hind-limb morphology and perch diameter. The relationship identified between behavior and density of surrounding saplings may indicate the importance of additional perches that individuals can access for refuge and/or to undertake social interactions (Hertz 1974). We do not think that defense is related to basking, because *N. polylepis* is a thermoconforming, non-basking species the body temperature of which is best explained by the ambient temperature of the surrounding habitat (Hertz 1974). Body size, in contrast, influences fighting ability in anoles (Tokarz, 1985) and other animals (Johnsson *et al*. 1999). Tokarz (1985) found that larger male *N. sagrei* defended their perch sites more successfully than smaller males because the larger lizards have more challenging displays. Given similar sizes of intruders and residents in this study, body size should not influence agonistic behaviors.

Other studies have also documented that agonistic behaviors differ depending on habitat resources. In a laboratory experiment with Brown Trout (*Salmo trutta*), individuals in habitats with the preferred substrate initiate attacks toward conspecific intruders faster and more frequently than do residents of habitats with less preferred substrate (Johnsson *et al*. 2000). Crayfish increase aggressive behavior when in the presence of food and shelter (Moore 2007). And last, Camfield (2006) documented that territory owners in two species of hummingbirds defended artificial feeders with higher levels of sucrose more intensely than feeders with low sucrose levels.

Based on our findings about the mechanisms driving variation in aggressive behaviors in *Norops polylepis*, we suggest that manipulative experimental studies are needed to test the ways in which resident male anoles prioritize defense of perches. It also would be useful to evaluate the influence of the presence of females, population density, and previous social history on agonistic behavior to contribute to a model construct for understanding the behavior of *N. polylepis,* as well as other anoles.

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