
ASSESSING THE RELATIVE IMPORTANCE OF INTRASPECIFIC AND INTERSPECIFIC INTERACTIONS ON THE ECOLOGY OF *ANOLIS NEBULOSUS* LIZARDS FROM AN ISLAND VS. A MAINLAND POPULATION

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Abstract.—Predation and competition are key ecological interactions that may drive island syndrome characteristics. However, the relative importance of these interactions in island and mainland environments is debated. We used *Anolis nebulosus* inhabiting a region lacking congeneric species on the coast of Jalisco, Mexico, as a model to elucidate the ecological role of intraspecific and interspecific competition for an insular population and a mainland population. We conducted surveys to determine densities of anole and other lizard species at both sites. We also carried out capture-mark-recapture of anoles to determine survival and frequency of caudal damage. In addition, we used video-recordings of focal anoles to determine rates of intraspecific and interspecific encounters and aggression, with higher rates suggesting greater competition, and determined direct predation when focal anoles were eaten. We found a significantly higher density of *A. nebulosus* on the island. Rates of intraspecific encounters and aggression were also significantly higher on the island. By comparison, interspecific encounters and aggression with other lizard species, as well as caudal autotomy, were higher on the mainland. We obtained few direct observations of predation, all of which were on the mainland, with no predation observed on the island, and survival was similar between populations. Although we were limited by the fact that we had only one island and one mainland population, our results on lizard density and encounter rates provide evidence for these populations lacking congeneric species that intraspecific competition is stronger on the island than on the mainland, whereas interspecific competition is stronger on the mainland.

Key Words.—Aggression rates; capture-recapture survival modeling; caudal autotomy; encounter rates; island syndrome characteristics; video-recording

INTRODUCTION

Predation and competition (both interspecific and intraspecific) are key ecological interactions that may drive island syndrome characteristics, in which populations of species on islands may be of larger size, have higher growth rates, show later maturation, or lack sexual dimorphism, compared to populations of the same species on the mainland (Alder and Levins 1994; Losos 1994; Palkovacs 2003; Calsbeek and Cox 2010). However, debate has arisen as to the relative intensity and importance of these interactions in shaping populations of *Anolis* lizards in mainland and island environments (Palkovacs 2003; Calsbeek and Cox 2010; Losos and Pringle 2011). It has been suggested that these island syndrome characteristics are a result of decreased predation pressure, given that small islands have reduced species richness and consequently fewer

potential predator species than the mainland (Crowell 1986; Alder and Levins 1994; Palkovacs 2003). Predation rates on *Anolis* lizards, however, are not always lower on small islands, even though they have fewer species, as there may be a high abundance of one predator species or increased predator efficiency (Wright et al. 1984; McLaughlin and Roughgarden 1989).

Alternatively, competition may shape island populations, either by reduced interspecific competition enabling niche expansion and greater body size (Losos 1994; Palkovacs 2003; Kolbe et al. 2008) or through increased intraspecific competition in which larger individuals would have a competitive advantage (Pafilis et al. 2009a; Thomas et al. 2009; Calsbeek and Cox 2010; Itescu et al. 2016). Experimental manipulation of island populations of anole lizards by Calsbeek and Cox (2010) found that predation pressure altered lizard behavior and mortality rate, but that higher

anole population density, and consequently a greater probability of intraspecific encounters, resulted in larger body sizes. In this way, predation, and interspecific and intraspecific competition can influence the structure of lizard communities (Losos 1994; Calsbeek and Cox 2010; Losos and Pringle 2011).

However, studies have encountered difficulties in accurately estimating rates of predation and competition. In lizards, predation rate has been inferred from mortality rate (Wilson 1991; Calsbeek and Cox 2010), frequency of caudal autotomy (Pafilis et al. 2009b; Clobert et al. 2000), survival in presence of a potential predator (Schoener et al. 2002), or population density in the presence and absence of potential predators (Campbell et al. 2012). Interspecific competition has been inferred from inclusion or exclusion of competitors (Lister 1976; Leal et al. 1998; Langkilde et al. 2005; Losos 2008) or from modifications of several resources (Petren and Case 1998). Intraspecific competition has been inferred from aggression experiments in the laboratory (Raia et al. 2010), frequency of caudal autotomy (Pafilis et al. 2009a; Itescu et al. 2016), and supposed consequences in species attributes such as morphology, population density, and resource use (Thomas et al. 2009; Calsbeek and Cox 2010; Cote and Clobert 2010). Nevertheless, determining the relative importance of predation and competition in shaping populations requires direct testing of these interactions in mainland and island populations (Losos and Pringle 2011).

To elucidate the role of inter and intraspecific competition and predation in structuring communities of Clouded Anoles (*Anolis nebulosus*), we used video-cameras to directly quantify frequency of intraspecific and interspecific encounters and aggression, as well as predation rates, to test the hypothesis that intensity of competition (inter and intra) and predation differ between an island and a mainland population. Furthermore, we estimated population density, survival, and frequency of caudal autotomy to test the hypothesis of differing evolutionary drivers on the island and the mainland.

MATERIALS AND METHODS

Study site and species.—We conducted the study along the southwestern coast of Jalisco, Mexico, at a mainland site in the Chamela Biological Station (19°29'48"N, 105°02'25"W) of the Universidad Nacional Autónoma de México, and on the San Agustin Island (19°32'0.4" N, 105°05'18"W), known locally as San Panchito, located 5.5 km northwest of the Chamela Biological Station. Both study sites are located in protected areas. The Chamela Biological Station is part of the 13,142 ha Chamela-Cuixmala Biosphere Reserve, which contains 70 species of mammals, 270 birds, 19 amphibians, and 68 reptiles (Arizmendi et al. 1991; Garcia and Ceballos

1994; Ceballos and Miranda 2000). San Agustin Island comprises an area of 3.3 ha (280 m length and 230 m width) and is included within the Santuario de las Islas de la Bahía de Chamela, which comprises eight islands in the bay that combined maintain six species of bats, as well as 16 avian and seven reptile species (Comisión Nacional de Áreas Naturales Protegidas [CONANP] 2008). However, San Agustin Island has fewer species, with only four reptiles and no snakes recorded on the island (Andrés García, pers. obs.). The region is characterized by a strong seasonality in precipitation, where rainfall is concentrated from July to October, and there is an extended dry season that can last up to eight months (Bullock 1986). Average annual rainfall is 800 mm with a mean temperature of 24.9° C (Bullock 1986; Maass et al. 2017). The dominant vegetation at both sites is Tropical Deciduous Forest where the majority of trees drop their leaves during the dry season. However, trees are smaller on the insular site compared to the continental forest (CONANP 2008). Of the eight islands and four islets in Chamela Bay, only San Agustin Island has mature dry forest vegetation and is the only island on which anole lizards have been recorded (Andrés García, pers. obs.); therefore it was not possible to replicate the study on other islands within the bay.

Anolis nebulosus is endemic to Mexico and is distributed along the Pacific coastal plain, as well as in the Sierra Madre Occidental, the Balsas River Basin, and part of the Mexican Transvolcanic Belt (Garcia and Ceballos 1994; International Union for the Conservation of Nature [IUCN]. 2007. *Anolis nebulosus*. The IUCN Red List of Threatened Species. Available at www.iucnredlist.org/pdf/link.12752241 [Accessed 22 January 2017]). The species is a small, insectivorous lizard that is predominantly arboreal, but forages from ground-level to the canopy (Lister and García 1992). The average snout-vent length (SVL) is 42 mm in males and 36 mm in females, with average body weight of 1.7 g and 1.6 g, respectively (Garcia and Ceballos 1994).

Population density and survival.—We estimated population density and survival rates of *A. nebulosus* on both the island and the mainland using capture-mark-recapture (Zuñiga-Vega 2011). At each site, we established three survey quadrants of 25 × 25 m that we intensively surveyed for lizards on each of 2–3 consecutive days, every 2–3 mo from October 2010 to August 2012, giving a total of 30 surveys in each quadrant (45 h per quadrant), over a total of 10 survey periods. During each survey we captured anoles to determine their sex by the presence (males) or absence (females) of the dewlap. On first capture, we created an individual mark on each lizard by clipping a maximum of two distal phalanges that are free of lamellae per limb (Philip Medica et al., unpubl. report) to minimize any

potential impact on lizards. In addition, we recorded whether the tail had broken off, which has been used as an indicator of predation pressure (Cooper and Wilson 2008) and intraspecific aggression (Pafilis et al. 2009a; Itescu et al. 2016). We also recorded the number of individuals of other lizard species that we observed during our surveys to estimate the abundance of potential interspecific competitors for *A. nebulosus*.

Direct behavioral observations.—We recorded frequency of intraspecific and interspecific encounters and aggression, as well as events of predation, by direct observation. We conducted observations on three consecutive days every 2 mo, over the 2-y period, on both the island and the mainland. Each day we tethered an adult lizard at each of three perch heights (20 cm, 150 cm, and 200 cm) using a 15 cm-long thread that was tied around the pelvis of each focal lizard and attached to a branch or trunk of the tree. We used a SONY digital high definition camera (DCR-SX43, Sony Corporation, Tokyo, Japan) located 2 m away to film lizards for no more than 4 h during daylight between 0900 and 1500. Each lizard was used only once for these direct observations, then released at the site of capture (except for three individuals that were predated). In this way, we obtained 519.6 h of video-recordings of 111 *A. nebulosus* lizards, of which 68 individuals were from the mainland (343 h), and 43 individuals from the island (176.6 h).

We reviewed the video recordings to register data in the following categories: (1) predation, when the lizard was attacked and devoured; (2) interspecific encounter, when an individual of another species (not necessarily a lizard) approached within 2 m of the focal anole, which usually moved to avoid physical contact; (3) intraspecific encounter, when another anole of the same species approached the focal anole, which also usually moved to avoid physical contact; (4) interspecific aggression, when an individual of another species attacked (physical contact) the focal anole; and (5) intraspecific aggression, when another anole of the same species attacked the focal anole. For each video-recording, we divided the total number of events of each behavioral category by the duration of the video-recording to obtain the rates of predation and of interspecific and intraspecific encounters and aggression for each observation period of a focal lizard.

Data analyses.—To estimate anole population density, we used the Schnabel multiple recapture method (Ricker 1975), which has been used previously to calculate density of anoles (Lister 1981). We calculated anole density per ha for each survey period on both the island and the mainland, and determined normality of data using the Kolmogorov-Smirnov test.

We compared population density of anoles between the island and the mainland using a two-tailed t-test. We did not estimate density for the first survey period (October 2010) because recaptures of previously marked animals are needed to estimate this demographic parameter.

To estimate density of other lizard species that may compete with *A. nebulosus* in the island and the mainland, we divided the number of observed individuals of each of these species by the total area of the quadrants (1,875 m²), which we multiplied by 10,000 to report individuals per hectare (ind/ha). In this case, we conducted statistical analyses with density estimates from all survey periods per site. To adjust our estimates, we used the probability of detection calculated with occupancy models implemented with the software PRESENCE (U.S. Geological Survey and Colorado State University, Colorado, USA; MacKenzie et al. 2006). Occupancy models are based on repeated visits to observation sites to estimate by means of likelihood procedures the probability that an individual of a certain species is detected given that it is present at the site (MacKenzie et al. 2006). We thereby divided the number of individuals of other species observed in the study sites by the species-specific encounter probability (Armstrong et al. 2005).

Survival estimates.—We captured and marked 316 lizards on the island and 100 on the mainland. We used individual records of capture and recapture to estimate monthly survival probabilities using maximum likelihood procedures implemented in the software MARK (Colorado State University, Colorado, USA; Lebreton et al. 1992; White and Burnham 1999). We used a Cormack-Jolly-Seber framework to estimate both survival (ϕ) and recapture (p) probabilities. We built different competing models to test for different sources of variation in these two parameters. Our main purpose was to compare monthly survival between island and mainland populations. Thus, we tested for the effect of site on ϕ . We also attempted to test for differences between sexes. However, our sample size for the mainland was not large enough to detect intersexual variation; therefore, we only tested for the effect of sex for lizards in the island. With respect to p , we tested for effects of site, sex (again only for the island), and time (i.e., a different recapture probability for each sampling occasion). We also considered interactions between these factors affecting p . In addition, we included null models (constant ϕ and/or p) in our candidate model set.

We used the Akaike information criterion adjusted for small sample sizes (AIC_c) to identify the models that provided the best fit to our mark-recapture data (Akaike 1973; Burnham and Anderson 2002). The best-fitting model is identified by the smallest AIC_c value. However, a difference in AIC_c (Δ AIC_c) scores between two models

TABLE 1. Model selection results for mark-recapture data of *Anolis nebulosus* from an island and mainland populations in western Mexico. Monthly survival (ϕ) may differ between sexes (only in the island), between sites (island and mainland) or may be constant (.) across sexes and sites. Recapture rate (p) may differ between sexes (again in this case only in the island), between sites, among sampling occasions (temporal) or be constant (.) across sexes, sites, and sampling occasions. Models are ordered according to the Akaike information criterion adjusted for small sample sizes (AIC_c), from the model with the strongest support to that with the weakest support. We also report here the difference in AIC_c scores between each model and the best-fitting model (ΔAIC_c) as well as the Akaike weights (w), which indicate the relative support for each model in the data.

Model	AIC_c	ΔAIC_c	w
$\phi(\text{sex and site})p(\text{temporal})$	921.14	0	0.33
$\phi(\text{site})p(\text{temporal})$	921.36	0.22	0.3
$\phi(.)p(\text{temporal})$	922.18	1.04	0.2
$\phi(\text{sex and site})p(\text{temporal} \times \text{site})$	924.56	3.41	0.06
$\phi(\text{site})p(\text{temporal} \times \text{site})$	924.67	3.53	0.06
$\phi(.)p(\text{temporal} \times \text{site})$	924.68	3.54	0.06
$\phi(\text{sex and site})p(.)$	931.44	10.29	0.002
$\phi(\text{site})p(.)$	931.68	10.54	0.002
$\phi(.)p(.)$	932.99	11.84	0.001
$\phi(\text{sex and site})p(\text{site})$	933.2	12.06	0.001
$\phi(\text{site})p(\text{site})$	933.42	12.27	0.001
$\phi(\text{sex and site})p(\text{sex and site})$	933.68	12.54	0.001
$\phi(.)p(\text{site})$	934.29	13.15	0
$\phi(\text{site})p(\text{sex and site})$	935.45	14.31	0
$\phi(.)p(\text{sex and site})$	936.31	15.17	0
$\phi(.)p(\text{temporal} \times \text{sex and site})$	936.38	15.24	0
$\phi(\text{site})p(\text{temporal} \times \text{sex and site})$	936.44	15.3	0
$\phi(\text{sex and site})p(\text{temporal} \times \text{sex and site})$	936.89	15.75	0

smaller than two units indicates similar support in the data. Hence, all models with $\Delta AIC_c < 2$ with respect to the best-fitting model were also considered as strongly supported by the data. We further calculated Akaike weights (w), which are measures of relative support for each competing model (Amstrup et al. 2005). Based on these model weights, we calculated model-weighted averages for both ϕ and p , which incorporate the uncertainty in the process of model selection by considering the relative support for each competing model (Burnham and Anderson 2002). Therefore, these model-weighted estimates are more robust than those derived from any single model (Johnson and Omland 2004).

Rates of predation, encounter, and aggression.—To evaluate significance of rates of predation, interspecific and intraspecific encounters, and aggression obtained from the video-recordings, we generated 84%

bootstrap confidence intervals with 1,000 replications (MacGregor-Fors and Payton 2013) for each type of interaction (encounter or aggression) for each population. We considered a significant difference in predation and encounter and aggression rates where confidence intervals did not overlap between island and mainland sites (MacGregor-Fors and Payton 2013). Finally, we also used the Kruskal-Wallis test to compare the frequency of caudal autotomy in each sampling period among six categories: females, juveniles, and males from the island and the mainland. In all tests, we used a $P \leq 0.05$ significance level, and performed the analyses using the software STATISTICA (STAT Soft, Tulsa, Oklahoma, USA).

RESULTS

Population density and survival.—Density of *A. nebulosus* in each survey period differed significantly between the island and the mainland ($t = 4.39$, $df = 16$, $P < 0.001$), being on average two times higher on the island (mean = 518 ± 55 [SE] ind/ha) than the mainland (mean = 250 ± 24 ind/ha). On the island, we captured 157 males and 159 females, and recaptured 53 males and 41 females. In the mainland, we captured 100 individuals with 11 recaptures. Mean monthly survival rate of males (mean = 0.87, 95% CI = 0.83–0.90) and females (mean = 0.85, 95% CI = 0.81–0.89) were also higher on the island than for all individuals on the mainland (mean = 0.80, 95% CI = 0.66–0.89), although the high degree of overlap in 95% confidence intervals suggests that this difference was not significant. The best-fitting model for monthly survival rate had 33% of relative support in the data, and indicated differences between males and females on the island, and between the island and mainland, with temporal variation in recapture rate (Table 1). However, there were two competing models with $\Delta AIC_c < 2$. Of these, the second best-fitting model had 30% relative support in the data, and indicated a difference in survival between sites, with no differences between sexes on the island (Table 1). The third best-fitting model had 20% relative support, and indicated constant survival rate with no effect of site or sex (Table 1). According to all three models, recapture rate varied among sampling occasions without effects of sex or site (Table 1).

We observed another five lizard species on the mainland: the Cope's Largescale Spiny Lizard (*Sceloporus utiformis*), the Black-nosed Lizard (*Sceloporus melanorhinus*), the Colima Giant Whiptail (*Aspidoscelis communis*), the Many-lined Whiptail (*Aspidoscelis lineattissimus*), and the Tropical Tree Lizard (*Urosaurus bicarinatus*), whereas on the island we observed only two additional species: *A. lineattissimus* and *U. bicarinatus*. The lizard species with highest

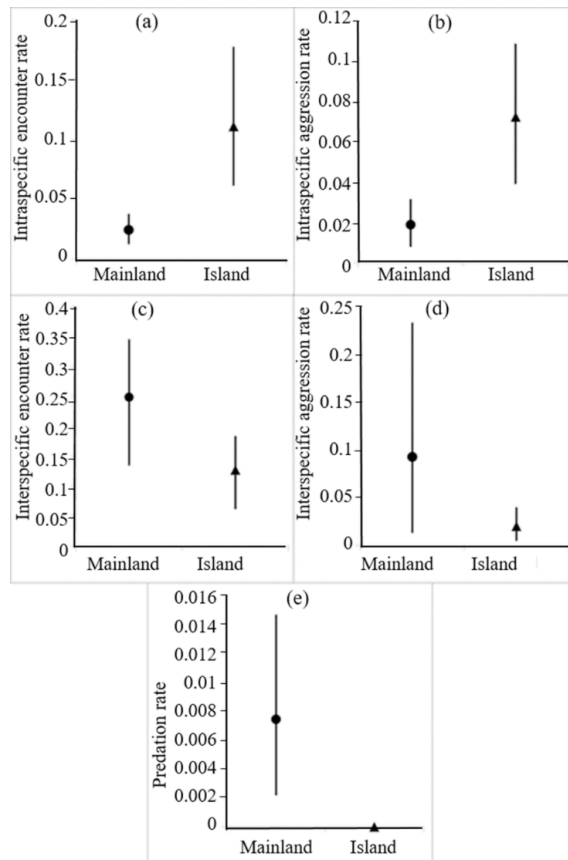


FIGURE 1. Rates of interspecific and intraspecific encounter and aggression, and predation per hour, with 84% bootstrap confidence intervals, obtained from video-recordings of focal *Anolis nebulosus* lizards inhabiting an island (triangles) and the mainland (circles) in western Mexico. Symbols are means and error bars represent 84% confidence intervals where non-overlapping confidence intervals indicate significant differences.

density on the mainland was *A. lineattissimus* (mean = 91 ± 32 ind/ha) followed by *S. utiformis* (mean = 44 ± 15 ind/ha), *S. melanorhinus* (mean = 31 ± 8 ind/ha), *U. bicarinatus* (mean = 32 ± 11 ind/ha) and *A. communis* (mean = 46 ± 18 ind/ha). On the island, the density of *A. lineattissimus* (mean = 107 ± 27 ind/ha) was higher than that of *U. bicarinatus* (mean = 97 ± 27 ind/ha). Both species occurred at higher densities than recorded on the mainland; however, this difference between island and mainland sites in density of other lizard species estimated for each survey period was only significant for *U. bicarinatus* ($t = 2.98$, $df = 18$, $P = 0.008$), whereas density of *A. lineattissimus* was not significantly different between island and mainland sites ($t = 0.90$, $df = 18$, $P = 0.379$).

Behavioral interactions.—Analysis of video-recordings of focal anoles revealed that rates of intraspecific encounters and aggression per hour were

4-5 times higher for lizards on the island compared to the mainland (Fig. 1a, b). Moreover, rates of intraspecific encounter and aggression were significantly higher on the island compared to the mainland (Fig. 1a, b). By comparison, rates of interspecific encounter and aggression tended to be higher on the mainland than the island (Fig. 1c, d), but this was not significant. On the island, three species (*A. lineattissimus*, *Hemidactylus frenatus* [Common House Gecko], and *U. bicarinatus*) interacted with *A. nebulosus*, whereas on the mainland nine species interacted with focal anoles (five lizards: *A. lineattissimus*, *A. communis*, *S. melanorhinus*, *S. utiformis*, *U. bicarinatus*; three bird species: the Inca Dove (*Columbina inca*), the San Blas Jay (*Cyanocorax sanblasianus*), and the White-winged Dove (*Zenaidura asiatica*); and one snake, the Brown Vine Snake (*Oxybelis aeneus*).

In general, predation rate per hour determined from video-recordings was extremely low, but differed significantly between island and mainland populations because predation was only recorded on the mainland (Fig. 1e). Of 68 anoles recorded on the mainland, we registered only three events of predation, one each by: *O. aeneus*, *C. sanblasianus*, and *S. melanorhinus* (previously considered strictly insectivorous; Siliceo-Cantero and García 2013). We also recorded 31 encounter events (23 interspecific and eight intraspecific), and 14 aggression events (eight interspecific and six intraspecific). For the 43 focal anole lizards video-recorded on the island, we recorded no predation events, but recorded 25 encounter events (14 interspecific, and 11 intraspecific), and 13 aggressive events (three interspecific and 10 intraspecific). The frequency of caudal autotomy also differed significantly among the six anole group categories ($\chi^2 = 11.53$, $df = 5$, $P = 0.031$). A higher percentage of individuals presented caudal autotomy on the mainland than on the island (Table 2). Furthermore, at both sites females had higher percentage caudal autotomy than males or juveniles (Table 2).

DISCUSSION

We found significantly higher density of *Anolis nebulosus* lizards on the island than on the mainland. Rates of intraspecific encounter and aggression, which may be indicative of intraspecific competition, were also significantly higher for lizards on the island than the mainland. A high population density on the island would lead to enhanced levels of competition among *A. nebulosus* conspecifics for territories, thermoregulation sites (Kolbe et al. 2008), food resources (Losos 1994), and reproductive mates (Lailvaux et al. 2004). This may increase territoriality of *A. nebulosus* on the island, permitting exclusive access to resources, being manifested in an increased frequency of behavioral

TABLE 2. Percentage of *Anolis nebulosus* lizards with broken tails from two island and mainland populations in western Mexico.

	Total Number of Individuals	Number of Broken Tails	% of Lizards with Broken Tails
Total	592	40	6.76
Island Total	487	28	5.75
Insular males	202	7	3.47
Insular females	169	16	9.47
Insular juveniles	116	5	4.31
Mainland Total	105	12	11.43
Mainland males	45	4	8.89
Mainland females	28	7	25.00
Mainland juveniles	32	1	3.13

displays, greater aggressiveness of insular individuals, and even direct attacks. Our results therefore suggest that intraspecific competition is stronger for the *A. nebulosus* population on the island than for the population on the mainland.

By comparison, rates of interspecific interactions and aggression were 3–4 times higher on the mainland than on the island, but the difference was not significant. We registered a greater diversity of lizard species during surveys on the mainland that could compete with anoles at this site, and our video-recording data showed more species interacting with focal anoles on the mainland than on the island. This is similar to published inventories for both sites, and demonstrates higher reptile species richness on the mainland than on the island (Garcia and Ceballos 1994; CONANP 2008). Therefore, a greater number of species could compete with the mainland *A. nebulosus* population for food resources, refuges, and thermoregulation sites. Hence, our results suggest that interspecific competition, potentially even leading to predation, is stronger for the mainland population than for anole lizards on the island.

Congeneric competition has been recognized as an evolutionary driver in anoles from the Caribbean islands (Losos and Pringle 2011). However, the *A. nebulosus* populations in our study inhabit a region lacking species of the same genus. Hence, in the absence of competition among congeneric species, other interactions such as predation, intraspecific and interspecific (non-congeneric) competition could have greater importance as evolutionary drivers shaping the ecology and structure of the island and mainland populations of our study.

Finally, direct observations of focal lizards during the morning-afternoon time period indicated a low predation rate on the mainland with no predation observed on the island. This may suggest that predation is not strong for *A. nebulosus* populations in our region. However, our field observations were biased towards

the morning hours, excluding the late afternoon when lizards are still active (Lister and Garcia 1992). We also did not conduct observations at night when several nocturnal snakes forage (Garcia and Ceballos 1994; Ramirez-Bautista 1994) that are potential predators of *A. nebulosus* (Mckinney and Ballinger 1966; Garcia and Ceballos 1994; Downes and Shine 2001; Campbell et al. 2012). Another source of bias could be the restricted movement imposed on our focal lizards, which was necessary to maintain the lizard in view of the camera, but which also reduced movements that may attract a predator. Nevertheless, this anole species is characterized by its cryptic behavior when at risk of predation, a low rate of movement, and the use of a sit-and-wait foraging strategy (Lister and Garcia 1992). Furthermore, the longitude of the 15-cm thread allowed anoles some liberty of movement.

Given these limitations, it is possible that predation rate is higher than detected by our direct observations, but there is still likely to be a low predation rate on the island. The small size of San Agustin Island is not adequate to maintain a diversity of predator species, and we have never recorded snakes on the island over almost 10 y of surveys in this and other projects. In particular, the presence of snakes on small Caribbean islands was found to significantly decrease survival of anole lizards (Calsbeek and Cox 2010). The only potential predator species that we did record on the island were *Nephila* spiders, and *A. lineattissimus* lizards that predate anoles (Siliceo-Cantero and Garcia 2013). By contrast, the mainland site maintains a diversity of snakes, mammals, birds and arthropods (Arizmendi et al. 1991; Garcia and Ceballos 1994; Ceballos and Miranda 2000) that are potential predators for anoles.

The use of video-cameras to record ecological interactions in our study enabled direct observations of the type and frequency of interactions taking place. Most studies use indirect measures to infer rates of predation or competition (Wright et al. 1984; Clobert et al. 2000; Calsbeek and Cox 2010). However, video-cameras have been used to estimate rates of ecological interactions in studies of avian nest predation rates (Sanders and Maloney 2002; Williams and Wood 2002; Stake and Cimprich 2003; Thompson and Burhans 2003), predator-prey encounter rates of fish (Turesson and Brönmark 2007), and contact rates of Elk, *Cervus elaphus* (Creech et al. 2012). Therefore, we consider that the results obtained in our study are close to the real scenario, and support conclusions of other studies that predation rates are low on small islands compared to the mainland or large islands (Alder and Levins 1994; Palkovacs 2003), and that competition, rather than predation, could be the main evolutionary driver of the ecology of insular anole populations (Losos 1994, 2009; Calsbeek and Cox 2010; Losos and Pringle 2011).

Caudal autotomy and survivorship.—Caudal autotomy was significantly higher for the mainland *Anolis nebulosus* population compared to the insular population, and this difference in frequency of caudal autotomy may reflect differing scenarios at each site. Caudal autotomy has been used as a proxy indicating predation pressure (Clobert et al. 2000; Pafilis et al. 2009a). However, in our direct observations we recorded few predation events, but a higher frequency of interspecific encounters and aggression of *A. nebulosus* individuals with other lizard species on the mainland.

On the other hand, for the insular population, caudal autotomy may reflect rates of intraspecific aggression under the conditions of high population density, and low predator richness on that site (Itescu et al. 2016). For the *A. nebulosus* population from San Agustín Island, we recorded a high frequency of intraspecific encounters and aggression in direct observations. Therefore, tail autotomy on the island may be the result of intraspecific competition arising from the high population density that we recorded at this site. Hence, as suggested by Itescu et al. (2016), the high frequency of caudal autotomy for mainland *A. nebulosus* may reflect greater pressure from interspecific competition, as well as some predation pressure, whereas for insular populations the frequency of caudal autotomy may reflect pressure from intraspecific competition under high population densities.

Our mark-recapture analysis indicates that survival rates of *A. nebulosus* are similar between the island and the mainland. This is an intriguing result because several studies have demonstrated higher survival on islands usually associated with lower abundance of predators (Palkovacs 2003; Schoener et al. 2005). According to our evidence, the source of mortality might differ between the island and the mainland, with agonistic intraspecific encounters and competition for limited resources promoting mortality in the island population, and predation and aggressive encounters with other lizard species promoting mortality in the mainland population. The intensity of intraspecific interactions observed for the insular population may be strong enough to produce similar mortality rates to that observed on the mainland, where there are more predator species (Arizmendi et al. 1991; García and Ceballos 1994; Ceballos and Miranda 2000; CONANP 2008), and where we clearly observed predation events. Nevertheless, we recognize that the number of lizards that we captured, marked, and recaptured in the mainland was too low to yield a more precise estimate of survival for this population. Hence, we cannot disregard the possibility that survival of *A. nebulosus* may be lower on the mainland than the island.

Concluding remarks.—Although we compared only one mainland to one island population, our study employs a valuable natural experiment of a system that has evolved in the absence of congeneric species and contributes to understanding of the differing roles of ecological processes in shaping animal communities. Our results indicate that the ecological processes of intraspecific and interspecific competition differ between these populations of anoles. Intraspecific competition was significantly stronger for the island anole population than the population on the mainland, whereas on the mainland, interspecific competition and/or predation tended to be higher than for anoles on the island. Nevertheless, these processes may have similar consequences in terms of survival.

These differences in interactions among populations on the island and on the mainland could promote morphological differences between mainland and insular populations, and also within populations. Two morphotypes have recently been reported for *Anolis nebulosus* in the region (Siliceo-Cantero et al. 2016), although this also could be promoted by the lack of congeneric competition. Food resource availability does not appear to be a factor in shaping populations, as a previous study conducted on this same population of *A. nebulosus* demonstrated that despite similar food availability between sites, mainland anoles have lower rates of body growth and lower body condition than island anoles (Siliceo-Cantero and García 2014). However, the island site has lower species richness, with fewer predators and interspecific competitors than the mainland site. Therefore, the selective environment differs between these two sites and also differs from the selective drivers of anole populations in the Caribbean (Losos 1994; Calsbeek and Cox 2010). In this way, our study suggests another possible scenario, where intraspecific competition on the island, and interspecific interactions of competition and/or predation on the mainland, could be the evolutionary drivers molding *Anolis* lizard populations, making this an intraguild reference system for evaluating evolutionary drivers in island lizard populations.

Acknowledgments.—We thank the graduate program for Biological Sciences at the Instituto de Biología (IB) of the Universidad Nacional Autónoma de México (UNAM), and the Estación de Biología Chamela from IB-UNAM. Our field work did not involve endangered or protected species, and complied with national laws regarding the use of wildlife for scientific research, being approved by the Secretaría del Medio Ambiente y Recursos Naturales, Mexico. The Dirección General

de Vida Silvestre of the Secretaría de Medio Ambiente y Recursos Naturales provided research permits for the study (permit number: SGPA/DGVS/05004/12).

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