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# Effects of age- and sex-specific density on behaviour and survival in a territorial lizard (*Anolis sagrei*)

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All organisms have specific habitat requirements that allow them to properly function in their environment. For many organisms, individuals shift habitat choice as they age because optimal habitats vary across life stages. Despite age-specific habitat use in a variety of taxa, identification of the causal factors driving such variation is limited by a lack of experimental studies. Field observations of the brown anole lizard, *Anolis sagrei*, show that juveniles use low, narrow perches whereas adults use relatively higher and thicker perches. We hypothesized that this variation is driven by interactions between age classes, rather than age-specific preference for microhabitat. We manipulated adult and juvenile densities in field enclosures with artificial trees to examine how inter-age class competition influences microhabitat choice. We predicted that juveniles would move to less desired microhabitats as adult density increased (i.e. individual behavioural response) and/or adults would negatively affect juvenile survival (via competition or cannibalism) in ways that would contribute to age-specific habitat use (i.e. natural selection). We found that adult males, but not females, reduced juvenile survival. However, neither adult male nor female density influenced juvenile microhabitat choice (i.e. perch height, width or substrate) via individual behavioural response or natural selection. We also tested whether juveniles influence adult microhabitat choice. As predicted, adults did not vary in microhabitat choice in response to juvenile presence. Our study provides a rare and robust assessment of the role of age- and sex-specific density in generating variation in behaviour and survival under natural conditions.

Individuals of different ages often vary in their habitat requirements (Dahlgren & Eggleston, 2000), and organisms shift habitat choice accordingly as they age (Montgomery, Lips, & Ray, 2011; Shine, Shine, & Shine, 2003; Stamps, 1983; Vagelli, 2004). However, most studies documenting these shifts are observational, and therefore cannot identify the causal factors of this variation. Nevertheless, many factors are responsible for ontogenetic variation in habitat use. For example, adults and juveniles may vary in resource needs (Hjelm, Persson, & Christensen, 2000) and/or performance (Irschick, Macrini, Koruba, & Forman, 2000, 2005), which differ across habitat types. Also, young animals are often at a greater risk of predation because of their lower levels of experience and smaller body sizes (Foster, Garcia, & Town, 1988; Werner & Hall, 1988). In addition, direct competition between adults and juveniles can result in one age class displacing another (Delaney & Warner, 2017; Keren-Rotem, Bouskila, & Geffen, 2006; Van Horne, 1982). Furthermore, competition between age classes can influence foraging efficiency (Milinski, 1982; Slotow & Paxinos, 1997) and predation risk (Keren-Rotem et al., 2006; Slotow & Paxinos, 1997). In most cases, juveniles are likely to be influenced by adults because of their smaller size and subordinate status (e.g. Smale, Frank, & Holekamp, 1993; Van Horne, 1982). In particular, juveniles of species that exhibit cannibalism may be especially motivated to move to habitats that reduce interactions with adults (i.e. individual behavioural response), and/or selection may favour juveniles that occur in areas of low adult density (i.e. natural selection; Keren-Rotem et al., 2006). Moreover, age class interactions may vary depending upon adult sex because males and females can vary dramatically in behaviour (Bjorkqvist, Osterman, & Lagerspetz, 1994), especially in species exhibiting sexual size dimorphism (Blanckenhorn, 2005; Perry, 1996). Understanding the ecology of each age class, sex, and their interactions will provide insight into the impact of different individuals in their environment (Irschick et al., 2005; Selander, 1966).

Competition for microhabitat has been an important driver of the adaptive radiation of the lizard genus *Anolis* throughout the

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Caribbean (Losos, 2009; Williams, 1983). Specifically, species are spatially partitioned across their habitats by utilizing variable heights and widths of arboreal perches; several studies show that this partitioning is a response to interspecific competition (Leal & Fleishman, 2002; Pacala & Roughgarden, 1982, 1985; Schoener, 1968; Stuart et al., 2014). However, despite extensive work on the interspecific variation in *Anolis* habitat use, much less is known about how individuals within a species partition microhabitat. The brown anole, *Anolis sagrei*, is well suited for addressing these issues for a number of reasons. First, this diurnal lizard often occurs at extremely high densities (Lee, Clayton, Eisenstein, & Perez, 1989; Schoener & Schoener, 1980), suggesting competition may influence microhabitat use. Second, *A. sagrei* conspicuously perch on vegetation and have high site fidelity (Calsbeek, 2009; Schoener & Schoener, 1982). This allows for repeated measurements of microhabitat choice for each individual. Third, juveniles use low, narrow perches at our study site in Ormond Beach, Florida, U.S.A., whereas adults occur on higher and thicker perches (Delaney & Warner, 2016), possibly due to adults forcing subordinate juveniles to less preferred microhabitats (Delaney & Warner, 2017). Fourth, adult *A. sagrei* are cannibalistic on young individuals (Cates et al., 2014; Gerber, 1999). Thus, competition with and predation by adults should place a strong incentive on juveniles to modify their behaviours in response to adult density.

We conducted two simultaneous experiments by manipulating adult and juvenile densities in field enclosures to examine the role of inter-age class competition in generating variation in microhabitat use in the lizard *A. sagrei*. The first experiment tested the influence of adult sex and density on juvenile microhabitat choice and survival. We hypothesized that adults would (1) force juveniles to less preferred microhabitat (i.e. individual behavioural response) and/or (2) be a selective agent against juveniles that use high, thick perches (i.e. natural selection). Also, because adult males are larger and more territorial than females, we predicted that adult males would exert a stronger influence on juvenile behaviour (via competition and/or cannibalism) than adult females. In contrast, because the presence of juveniles could influence adult behaviour, our second experiment was designed to assess the influence of juvenile presence on adult microhabitat choice. Aside from research on mammals with maternal care (Barten, Bowyer, & Jenkins, 2001; Stokke & Toit, 2002), little is known about how juvenile density affects adult behaviour in most animals. However, because adult *A. sagrei* are larger and likely more dominant than juveniles, we hypothesized that juvenile presence would have little to no influence on adult microhabitat use.

## METHODS

We assembled 27 mesh enclosures (0.61 × 0.61 × 1.83 m; Carolina Biological Supply Co., Burlington, NC, U.S.A.) on an island (Fig. 1a, Island A) in the Halifax River, Ormond Beach, Florida from 31 June to 7 July 2014. The open area in the centre of the island was homogeneous in habitat and reduced variation in ambient conditions among enclosures. Densities of free-ranging lizards were low in the open area (D. M. Delaney, personal observations) and thus reduced interactions between free-ranging lizards and individuals in the enclosures.

Each enclosure contained an artificial tree (~1.8 m tall) with perches that varied in height (42 cm, 84 cm, 126 cm, 168 cm) and diameter (0.32 cm, 0.64 cm, 1.27 cm, 1.9 cm, 2.54 cm), and had an artificial leaf glued to the distal end. Wooden fence posts were used as the ‘trunk’ of each tree, and horizontal perches were constructed from 15 cm long dowel rods (branches) that were attached perpendicularly to the trunk. Perches were radially arranged (spaced ~5 cm intervals) around the trunk, and the order of the five perch diameters was random at each of the four heights so that each perch height contained each perch diameter. The mesh enclosures allowed lizards to experience natural ambient conditions. We also tied shade cloth to the top of each enclosure to allow lizards to move between shaded and sunlit areas. The mesh allowed ample amounts of invertebrates into the enclosures, and both age classes of lizards were observed feeding on invertebrates. The floor of each cage was covered with linoleum (0.61 × 0.61 m) to prevent the tree from tearing holes in the mesh. Blinds with small holes cut at various heights were hung on the north side of each enclosure to allow the observer (D.M.D.) to approach and record behaviours without disturbing lizards. Enclosures were arranged in locations around the island so that individuals from one enclosure could not interact with individuals from other enclosures.

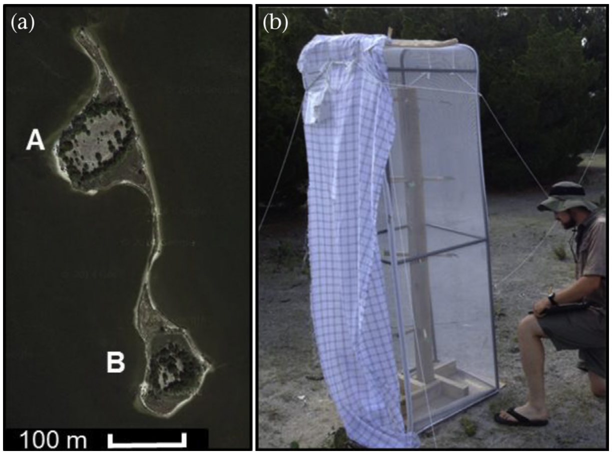

**Figure 1.** (a) Aerial photograph of the islands and (b) a ground-level photograph of an enclosure used in this study. Enclosures were constructed in the open central area on the northern island (labelled ‘A’), and lizards used for this study were collected on the southern island (labelled ‘B’).

*Anolis sagrei* ($N = 276$) were collected from a nearby island that was connected by a narrow sandbar (Fig. 1a, Island B). Lizards were collected 1–2 days before they were needed for the experiments. We measured snout–vent length (SVL) to the nearest 1 mm and mass to the nearest 0.01 g. Sex was determined by dorsal pattern and the presence (males) or absence (females) of enlarged postcloacal scales. Females <34 mm and males <39 mm SVL were classified as juveniles (mean ± SE = 22.53 ± 0.36 mm, range 17–34 mm) and those larger were classified as adults (51.98 ± 0.50 mm, range 42–64 mm; Lee et al., 1989). Toes were clipped with sterilized surgical scissors, without analgesic, to uniquely mark each individual. No more than one toe was clipped from each limb, and toes were clipped distal to toe pads to minimize any effect on locomotor ability. Such marking methods are quick and cause no increase in corticosterone in another lizard, *Eulamprus heatwolei* (Langkilde & Shine, 2006). Identification numbers were written on the lateral surfaces of adults (using a sharpie marker) so they could be visually identified in the enclosures without disturbance. Because juveniles were too small to write legible ID numbers, we placed dots of different coloured acrylic paint on their dorsums for unique visual identification. After lizards were measured and marked, individuals were haphazardly assigned to one of nine treatments (Table 1) divided among two experiments, which occurred simultaneously. The first experiment examined the effects of adult density and sex on juvenile microhabitat choice and survival; the second experiment examined the