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Monogamy, Polygyny and Interspecific Interactions in the Lizards *Anolis pogus* and *Anolis gingivinus*

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Polygyny is the most common mating system in lizards. Stamps (1983) compiled data on the male/female home-range ratio of nine *Anolis* species during the breeding season and found that in eight of these species males had home ranges at least three times larger than females, thus suggesting a high degree of polygyny in the genus. The exception was *A. distichus*, with a male/female home-range ratio of 1.15 (Schoener and Schoener, 1980).

The male/female home-range ratio is an indirect measure of polygyny and can be misleading. For example, despite a male/female home-range ratio of 3.2 in *A. nebulosus*, Jenssen (1970) suggested, based on the geometry of the home ranges, that this species had a semi-monogamous breeding structure. Thus, if male home ranges overlap little, as is the case for most *Anolis* (Stamps, 1977b), a more precise measure of polygyny is how many females are in the home range of each male. Ranges for this measure have been reported in a few cases: 0-8 females/male in *A. aeneus* (Stamps, 1977a), 2-6 in *A. carolinensis* (Jenssen and Nunez, 1998), 0-4 in *A. cupreus* (Fleming and Hooker, 1975) and 0-5 in *A. garmani* (Trivers, 1976). Therefore, out of five *Anolis* studies that analyzed the geometry of home ranges, four reported a polygynous social structure.

We present data on a new case of a monogamous *Anolis* species, *A. pogus*, and on the social system of sympatric *A. gingivinus*, on St. Martin, Lesser Antilles. The two species are closely related, both belong to the *bimaculatus* group (Lazell, 1972; Roughgarden, 1995), but differ in sexual dimorphism [male/female ratio of the maximum snout-vent length (MSVL) is 1.36 for *A. gingivinus* and 1.19 for *A. pogus*].

We also suggest the presence of interspecific territoriality between *A. gingivinus* and *A. pogus*. Of eight Lesser Antillean islands with two *Anolis* species, in St. Martin the species are closest in size (*A. gingivinus* MSVL=72 mm, *A. pogus* MSVL=50 mm) occupying similar ecological niches (Roughgarden, 1995). Interspecific territoriality has been well documented for birds (Griffis and Jaeger, 1998), but data on reptiles is lacking.

We monitored space use and behavioral interactions of *A. pogus* and *A. gingivinus* at two sites, Puit Paradis and Pic Paradis, from 16-24 July 1998. Both sites are mesic and are covered by broadleaf woodland. At Puit Paradis, we laid a 9.6 × 7.2 m² horizontal grid, with individual grid cells of 1.2 × 1.2 m². At Pic Paradis we laid a 3.9 × 2.7 m² horizontal grid with indi-

vidual grid cells of $0.6 \times 0.6 \text{ m}^2$. Grid cells were delimited with nylon lines attached to a flagging tape that marked the periphery of the grid. Vertical reference points were painted at 1 m and 2 m height on trees and shrubs in the grids. Lizards were marked with a long blade of grass tipped in water-based paint, and were not captured to minimize disturbance. The position of the paint mark allowed the identification of each individual.

Observations were conducted in one or two daily sessions lasting 2-3 h, from 0930-1630 hrs, for a total of 1615 minutes at Pic Paradis and 1230 minutes at Puit Paradis. We used scan samples to record the position of all individuals in each grid. The interval between scans was 5 min for Pic Paradis and 10 min for Puit Paradis. The X, Y, and Z positions were estimated to the nearest 0.3 m. Two-dimensional home ranges were estimated for individuals observed regularly (≥ 20 observations at Puit Paradis and ≥ 40 at Pic Paradis). Positions were ranked by frequency of use, and the positions contributing to the upper 90% of home range use were selected to draw a minimum convex polygon (White and Garrott, 1990). Tied ranks were resolved to minimize area.

We calculated intraspecific male-female, male-male and female-female three-dimensional home range overlaps. The home range overlap of lizard *a* with lizard *b* is the average of the proportion of time that lizard *a* spent in grid points also used by lizard *b* and the proportion of time that lizard *b* spent in grid points also used by lizard *a* (Smith and Dobson, 1994). We also calculated total interspecific overlaps; such overlap for lizard *a* is the sum of the overlaps between this lizard and each non-conspecific lizard. In addition, to compare our results with those of McCloskey and Hecnar (1994), we report total interspecific overlaps using their overlap measure (MCO), which measures the overlap of lizard *a* with lizard *b* as the proportion of grid points used by lizard *a* that are also used by lizard *b*.

Behavioral data were sampled continuously for all individuals and recorded during the scan samples. Five types of behavioral events were recorded: displays, displacements, chases, fights, and copulations. For displays, we recorded the individual performing the display, and if detected, the individual to whom the display was directed. For displacements, chases, and fights, we recorded the winner and the loser of the interaction (the loser was the animal that left the locale first). For copulations, we recorded the two lizards involved. Repeated events between two scan samples involving the same lizard pair were not recorded. All means are presented \pm one SE.

Social systems of Anolis pogus and A. gingivinus.—In *Anolis pogus*, each male home range was associated with one female home range (Figs. 1a, 2a). The home-range overlap within each male-female pair was extensive, averaging $91 \pm 4\%$ at Pic Paradis and $50 \pm 9\%$ at Puit Paradis. The higher overlap at Pic Paradis (*t*-test, $p = 0.008$) was probably due to the smaller home range sizes (Table 1, *t*-test, $p = 0.003$). The home-range size ratio between male and females was 1.05, averaged over both sites and weighted by the number of males in each site (Table 1).

Home ranges of male *A. pogus* rarely overlapped (highest male-male overlap was 3%). Female home

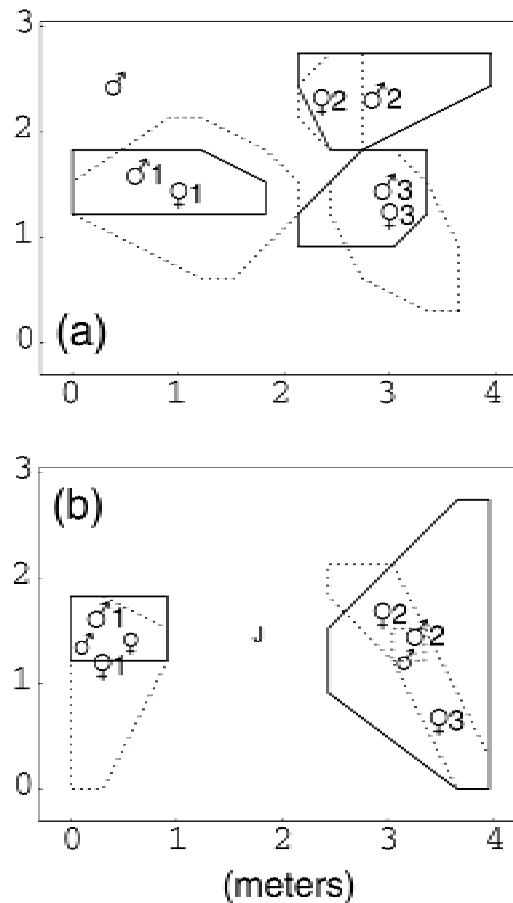


FIG. 1. Home ranges at Pic Paradis for males (—) and females (· · ·) with at least 40 observations. (a) Home ranges of *Anolis pogus*. (b) Home ranges of *Anolis gingivinus*. Labels indicate the mean position of each individual. J = juvenile. Individuals not numbered are individuals for which we had more than 6 but fewer than 40 observations.

ranges also overlapped little (highest female-female overlap was 9%). The highest overlap between a “non-paired” male and a female was 8%, which is seven times lower than the overlap between male-female pairs. One adult female without an adult male partner overlapped 37% with a juvenile (Fig. 2a).

The spatial organization of the home ranges and the male/female home-range ratio for *A. pogus* suggest the presence of a monogamous social system, which was supported by observed matings. At Pic Paradis we observed ten copulations, all within spatially associated pairs. At Puit Paradis we observed four copulations: three within pair and σ^6 with an unmarked female. With the exception of Puit Paradis’ pairs one and five, all pairs mated once or more. An average of two days elapsed between copulations, but 40% of the

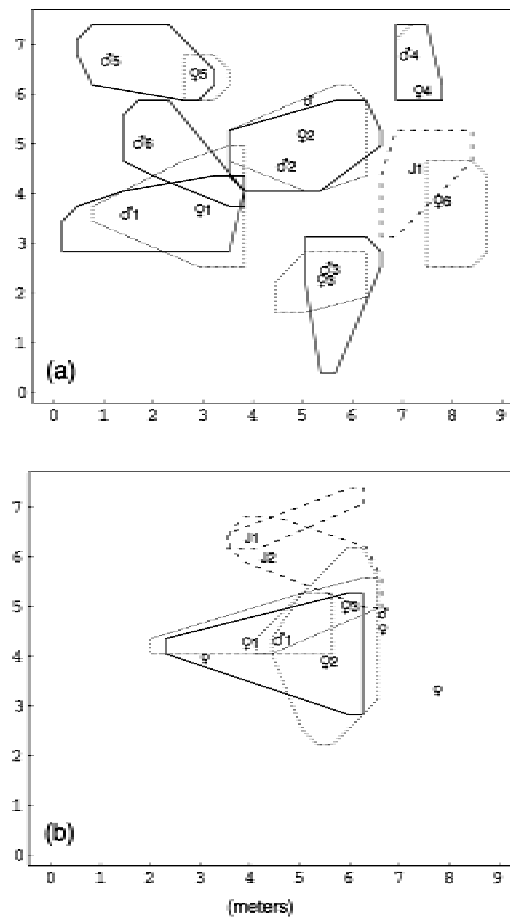


FIG. 2. Home ranges at Puit Paradis for males (—), females (· · ·) and juveniles (- - -) with at least 20 observations. (a) Home ranges of *Anolis pogus*. (b) Home ranges of *Anolis gingivinus*. Labels indicate the mean position of each individual. J= juvenile. Individuals not numbered were individuals for which we had more than 3 but fewer than 20 observations.

inter-copulatory durations were shorter than 3 h. This was surprising because laboratory experiments show that females of the polygynous *A. carolinensis* are not sexually receptive for at least 24 h after copulation (Crews, 1973) and as long as several days until ovulation (Crews, 1980).

The spatial organization of *A. gingivinus* home ranges (Figs. 1b, 2b) differed from that of *A. pogus*. At Pic Paradis, one male was associated with a single female but the other had two females in its home range. At Puit Paradis, the male had three females in its home range. Overlaps of each male with each female inside its home range averaged $81 \pm 2\%$ at Pic Paradis and $30 \pm 6\%$ at Puit Paradis, and were significantly lower than the male-female pair overlaps for *A. pogus* (after controlling for site; t-test, $p = 0.04$). The

male-female home-range size ratio was 2.6 (average over both sites, weighted by the number of males in each site, see Table 1).

Anolis gingivinus perched relatively high on trees and shrubs (Table 1). Each male home range encompassed one tree and was exclusive. We observed other males, but their presence was temporary (one or two days, unnumbered males in Figs. 1b, 2b). Females associated with the same male overlapped home ranges partially (54% female-female overlap at Pic Paradis and 15% mean female-female overlap at Puit Paradis).

The home range distribution and male/female home-range ratio of *A. gingivinus* are consistent with a polygynous social structure. However, we did not observe enough *A. gingivinus* matings to further assess the social system. We observed three copulations of ♂1 with ♀1 at Pic Paradis, and two copulations of the adult male with two females at Puit Paradis.

Stamps (1983) hypothesized that polygyny in territorial species is due to male-male competition for females; males defend large territories so that they have exclusive access to many females. Because selection for large size result from male-male competition, Stamps predicted that sexual size dimorphism (SSD) should be correlated with the degree of polygyny. Our data support this hypothesis: the smallest and less dimorphic *A. pogus* is monogamous, whereas the largest and more dimorphic *A. gingivinus* appears to be polygynous. It should be determined if the two closest relatives of *A. pogus* (*A. watsi* and *A. schwartzi*), which also have small sexual size dimorphisms, are monogamous.

The male-male competition hypothesis also states that polygyny is more likely when females are more clumped (Stamps et al., 1997). The inverse of the female home range size is a classic measure of how clumped females are (Stamps, 1983). This measure is ambiguous at our sites because female *A. gingivinus* home ranges at Pic Paradis were smaller than for *A. pogus*, and the reverse was true at Puit Paradis. However, *A. gingivinus* perched high on trees and a male controlling a tree is in a privileged position to monopolize all the females using the same tree. In contrast, *A. pogus* perches low (Table 1) on rocks and dead twigs scattered in the ground. Thus female *A. pogus* have a non-clumped distribution, making it difficult for a male to control more than one female.

Interspecific interactions. Total interspecific overlap of each *A. gingivinus* individual with *A. pogus* individuals averaged $113 \pm 15\%$ (MCO= 94%) at Pic Paradis and $41 \pm 20\%$ (MCO=30%) at Puit Paradis. Conversely, total interspecific overlap of each *A. pogus* individual with *A. gingivinus* individuals averaged $94 \pm 18\%$ (MCO=74%) at Pic Paradis and $19 \pm 7\%$ (MCO=18%) at Puit Paradis. Higher interspecific overlaps at Pic Paradis than at Puit Paradis (t-test, $p < 0.001$) were probably due to the higher density of individuals of both species at Pic Paradis (1.0 individuals/m²) than at Puit Paradis (0.3 individuals/m²).

Interspecific agonistic interactions and interspecific displays were common; 43% of the fights, chases, and displacements were interspecific (Table 2), as well as 26% of the 76 directed displays. *Anolis gingivinus* juveniles were consistently chased away by *A. pogus* males. *Anolis gingivinus* females had more balanced

TABLE 1. Home range sizes (mean \pm SE in m²) and mean perch heights (mean \pm SE in m) of *Anolis pogus* and *A. gingivinus* from two sites in St. Martin. n = number of individuals. J = juveniles. Mean number of observations per individual was 172 ± 24 at Pic Paradis and 81 ± 7 at Puit Paradis.

		Pic Paradis			Puit Paradis		
		n	Home range	Perch height	n	Home range	Perch height
<i>Anolis pogus</i>	♂	3	1.0 \pm 0.1	0.1 \pm 0.0	6	3.1 \pm 0.5	0.1 \pm 0.1
	♀	3	1.3 \pm 0.5	0.0 \pm 0.0	6	2.6 \pm 0.7	0.1 \pm 0.1
	J				1	2.6	0.0
<i>Anolis gingivinus</i>	♂	2	1.7 \pm 1.2	0.9 \pm 0.1	1	5.8	1.6
	♀	3	0.8 \pm 0.2	0.6 \pm 0.0	3	3.6 \pm 0.9	1.1 \pm 0.3
	J				2	2.2 \pm 1.0	0.1 \pm 0.0

and intense disputes with *A. pogus* males, but usually won over *A. pogus* females. *Anolis gingivinus* males were involved in only four interspecific agonistic interactions, and in one case the winner was the much smaller *A. pogus* male.

M'Closkey and Hecnar (1994) studied interspecific spatial overlap of five lizard species in different habitats in the Sonoran Desert and in the Colorado Plateau. They found that spatial overlap for each species pair varied from 13% to 223% and suggested that different species did not exhibit frequent interspecific interference. Although the interspecific overlaps for *A. gingivinus* and *A. pogus* are within this range, Pacala and Roughgarden (1982, 1985) reported interspecific competition between both species. Furthermore, agonistic interactions and displays between these species in our study accounted for about one third of all interactions; many occurring around feeding resources (e.g., fruits with insects) or when an individual invaded the main perch of a non-conspecific. If territoriality is defined as the exclusive use of part of the home range or as site-specific dominance (Maher and Lott, 1995), it can be argued that interspecific resource-based territoriality exists between *A. gingivinus* and *A. pogus*.

TABLE 2. Fights, chases, and displacements of *Anolis pogus* and *A. gingivinus* from two sites in St. Martin. The rows correspond to the animals winning the agonistic interaction and the columns to the animals losing the interaction. In interactions for which no winner was clearly identified, a score of 0.5 was given to both participants.

		<i>Anolis pogus</i>			<i>Anolis gingivinus</i>		
		♂	♀	J	♂	♀	J
		<i>Anolis pogus</i>	♂	14	3	0	1
	♀	0	1	1	0	0	0
	J	0	0	0	0	0	0
<i>Anolis gingivinus</i>	♂	2	1	0	0	8	1
	♀	7.5	7	0	0	13	1
	J	0	0	0	0	0	0

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