

SPATIAL AND BREEDING RELATIONSHIPS OF THE LIZARD, *ANOLIS CAROLINENSIS*: EVIDENCE OF INTRASEXUAL SELECTION

by

THOMAS A. JENSSEN¹⁾ and STEVEN C. NUNEZ²⁾

(Biology Department, Virginia Tech, Blacksburg Virginia 24061, USA)

(Acc. 28-VII-1998)

Summary

1. We used continuous 8-day monitoring to document the spatial and mating relationships of free-ranging *Anolis carolinensis* lizards at each of seven habitat-delineated study sites.
2. We found a polygynous social structure, consisting of a male and 2-6 resident females ($\bar{x} = 3.3$), on each site.
3. Spatially, both sexes utilized all available perch heights and diameters on the study sites (habitat generalists), though females tended to perch slightly higher and on significantly thinner substrata ($\bar{x} = 2.4$ m, 3.4 cm, respectively) than males ($\bar{x} = 2.3$ m, 5.3 cm, respectively).
4. Mean home range volume was eight fold greater for males (69 m^3) than females (8 m^3). Male home ranges were exclusive of other males (0% overlap), while neighboring female home range volumes overlapped an average of 18%.
5. Male snout-vent length (SVL) was positively correlated with male home range size (area, volume) and with number of resident females, but not with resident female SVL or resident female home range size.
6. Half of 397 male-female encounters led to close contacts in which males influenced courtship outcomes by: recognizing receptive and non-receptive females (differential display rate); bypassing 69% (85/123) of mating opportunities with receptive females; and copulating only when courtship was male-initiated.

¹⁾ Corresponding author.

²⁾ We thank K. Orrell, K. Ermland, and T. Tuchak for their assistance in the field, and R. Andrews, J. Congdon, M. Lovern, K. Orrell, K. Passek, and D. Ruby for their comments on the manuscript. Support came through J. Congdon and the Physiological Ecology Laboratory at the Savannah River Ecology Laboratory and the financial support by contract DE-AC09-76SROO-819 between the US Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

7. Larger males (who also had larger territories and more females) courted less per female, but with longer duration, and had longer copulatory durations than smaller males.
8. Male frequency of copulation (\bar{x} = once/1.4 days), however, had no correlates with measured variables; females were mated without bias to male or female attributes.
9. Male potential reproductive rate (PRR), estimated from the number of copulations with different females, positively correlated with male SVL. Female PRR, estimated from the inter-mating interval (*i.e.* the single-egg clutch interval), did not correlate with any measured male or female trait.
10. Our data, in concert with other field studies and *A. carolinensis* life history traits, document a polygynous mating system in which females seem to fit a 'no cost, neutral-mate-choice' model, and males (in response to sedentary, contiguously distributed females who clutch at weekly intervals over a 4-month period) employ territorial contests within an endurance rivalry as a prime mechanism for mate assortment.

Introduction

In his review of sexual selection, Andersson (1994) commented that studies have been biased toward intersexually selected mating systems, and more attention should be given to contest competition. In response to this opinion, we examine the relative effects of intra- and intersexual selection in the lizard, *Anolis carolinensis*. We selected this reptilian species because: (1) its life history and ecological traits predict an intrasexually selected reproductive system; (2) the behaviors of both males and females can be followed under natural settings; and (3) ultimately, phenotypic differences within each sex can be related to naturally occurring mating rates as a measure of sexual selection (Koenig & Albano, 1986). Furthermore, *A. carolinensis* has relatively few specialized traits or conditions which would complicate reproductive expression. The species lacks such factors as sympatric congeners (*e.g.* hybridization, interspecific competition), high vagility (*e.g.* migration, flight), high metabolic requirements (*e.g.* homeothermic costs), parental care (*e.g.* altricial dependency, incubation, viviparity, lactation), and specialized habitat, diet, and nesting requirements. Specifically, *A. carolinensis* is a habitat generalist (*e.g.* Jenssen *et al.*, 1995b, 1998), being widely distributed over a variety of microclimatic and arboreal habitats of southeastern United States (Conant, 1975), and has no endemic congeners (though eight exotic *Anolis* species are currently in Florida; Meshaka *et al.*, 1997). This lizard, with its low, reptilian metabolism (Jenssen

et al., 1996), meets its energetic needs by feeding infrequently from a wide variety of available arthropods (King, 1966; Jenssen *et al.*, 1995b; Nunez *et al.*, 1997). Females, laying single-egg clutches at weekly intervals over a 4-month breeding season, produce precocial neonates independent of parental care (Gordon, 1956; Fox, 1958; Licht, 1973; Smith *et al.*, 1973; Andrews, 1985a).

Besides a simple profile of life history and ecological traits, *A. carolinensis* exhibits characteristics suggestive of sexual selection. The species is sexually dimorphic in its morphology and behavior (Fitch, 1976; Jenssen *et al.*, 1995a, b; Nunez *et al.*, 1997), and practices territory-based polygyny (Ruby, 1984; Jenssen *et al.*, 1995b). Among the competing explanations for sexual dimorphism (*e.g.* see Stamps, 1983, 1995; Hedrick & Temeles, 1989; Shine, 1989), recent field data indicate that the intersexual differences of *A. carolinensis* best fit the predictions of the sexual selection hypothesis (Ruby, 1984; Jenssen *et al.*, 1995a; Nunez *et al.*, 1997). However, more information, particularly on the species' spatial and mating relationships, is needed to strengthen this inference and to suggest the relative expressions of intra- and intersexual selection in the *A. carolinensis* mating system.

For our study, we observed the spatial and reproductive relationships of unmanipulated, free-ranging *A. carolinensis* and used their naturally occurring behavior to characterize and quantify: (1) intersexual microhabitat utilization; (2) habitat volume required by individual lizards for shelter, food, and mates; (3) spatial relationships within natural groups of interbreeding lizards; (4) kinds, frequencies, and outcomes of courtship interactions within these breeding groups; (5) female inter-mating interval as an estimate of the inter-clutch interval (*i.e.* female potential reproductive rate, PRR, *sensu* Clutton-Brock & Parker, 1992); (6) male copulatory frequency with different females (*i.e.* male PRR); and (7) correlations of courtship and mating outcomes with the traits of individual males and females. From these data, we will suggest the extent to which males or females are directly controlling mate assortment. Our arguments will assume that male reproductive traits depend upon the distribution of reproductive females in space and time (Emlen & Oring, 1977; Cockburn, 1988; Davies, 1991), while female reproductive responses are constrained by life history and

ecological factors (Partridge & Endler, 1987; Stearns, 1992; Sutherland, 1996).

Methods

We collected data on breeding *A. carolinensis* from early May to late July 1993 along the Augusta canal (12 km northwest of Augusta, Georgia, USA) in a bottomland hardwood habitat typical of *A. carolinensis*. The physical characteristics of the canal were conducive to long-term focal observations and multiple scan sampling (Altmann, 1974) of free-ranging lizards. From an elevated tow path (3-4 m above the canal), we could observe the lizards as they moved in their arboreal home ranges within the vegetation which grew on the berm of the canal. The riparian habitat on the berm, consisting of trees and surrounding understory, was broken into clusters of arboreal vegetation by occasional patches of low, herbaceous vegetation. We used seven of these habitat clusters as separate study sites to record the spatial, social, and mating relationships among natural assemblages of lizards resident to the habitat clusters.

Each study site represented a large habitat cluster in which we had observed a territorial male. In an attempt to record all male-female interactions and matings, each site was monitored continuously for eight consecutive days (0830-1830 h) after all lizards within a study site had been marked. The study sites were sequentially observed, resulting in 56 days of observation (> 1200 observer h) before the end of the breeding season concluded our investigation. The study sites contained a total of seven resident adult males and 23 adult females, with respective mean snout-vent lengths (SVL) of 62.4 mm (\pm SE 1.31) and 50.3 mm (\pm SE 0.84). The lizards at each site proved to be natural complements of interbreeding lizards, and so we refer to the residents of each site as a "breeding group".

At each study site we captured, measured SVL, toe clipped, uniquely paint marked, and then released at their points of capture all observed lizards. The territorial male was continuously observed and the resident females were tracked by 30-min scan samples. Spatial relationships were marked at half hour intervals by recording the date and time of day, and each lizard's perch diameter, perch height, and three-dimensional position within the habitat (see below). Perch diameters were estimated to the nearest 0.5 cm as approximately referenced to the lizard's body length. Perch height was estimated to the nearest 0.25 m as referenced by a 7 m pole (marked in 0.5 m increments) placed against the tallest tree in the study site. In addition, we recorded ambient air temperature in the shade at 1.0 m (quick reading thermometer), and relative humidity (wet/dry bulb sling cyclometer). Half hour intervals were rated according to the proportion of cloud-free sunlight, where clear = > 25 min, partly cloudy = 5 - 25 min, and cloudy = < 5 min.

Home range volume and area were calculated with the scan samples of a lizard's spatial locations in the habitat. We estimated the X coordinate (width position) using a 20 m measuring tape (\pm 0.25 m) fixed along the tow path at the study site, the Y coordinate (depth position) using a range finder (\pm 0.2 m) while standing on the measuring tape at the corresponding X coordinate, and the Z coordinate (height position) using the vertical reference pole (\pm 0.25 m) mentioned previously. The scan samples of spatial locations (X, Y, Z positions) for each lizard at a study site were accumulated over an eight day period and transformed into a home range volume (m^3) using the methods in Nunez (1994). The con-

vex polygon method (Rose, 1982) was also used to calculate just the home range area (m^2) without regard to the Z coordinates. We will initially refer to male and female spatial data as defining home ranges. However, the home ranges are defended spaces (e.g. Jenssen *et al.*, 1995b; Nunez *et al.*, 1997), most obviously by males, and will be referred to as territories in the context of male social interactions.

For detailing intersexual contacts, we recorded individual identity, date and time of day, type of contact (types 1-4, see below), the individual who first moved toward the other (initiated contact), duration of contact, frequencies of courtship behaviors occurring during the contact, and copulations (if any) and their durations. We recognized the following four types of male/female contacts: type 1 — long range (terminated at distance), where the male and female came into sight distance of one another, but one or both moved off while still > 1 m apart; type 2 — short range (male terminated), where the pair approached (< 0.5 m apart), but the male moved off; type 3 — short range (female terminated), where the pair approached (< 0.5 m apart), but the female moved off; and type 4 — short range (lead to copulation), where the pair approached (< 0.5 m apart), and copulation subsequently resulted.

We used nonparametric statistics (Hollander & Wolfe, 1973) to test comparisons, and when appropriate, statistics were calculated using means from individual lizards as a single datum to better reflect population trends. Descriptive statistics are given as means (\bar{x}) with standard errors (SE). Data sets were analyzed using SAS procedures (SAS 1991).

Results

Habitat use

Both sexes used all available habitat on our study sites (habitat generalists), being found from ground level to the upper canopy, and from twigs and leaves to the largest tree trunks. The following intersexual comparisons emphasize to what extent the sexes shared a common set of habitat configurations. But as a caveat, the absolute values for the structural niche profile of *A. carolinensis* can be expected to vary across the variety of habitats in which the species is found.

Perch height

Most (65%) of 467 male perch heights ranged from 0-2 m, while most (80%) of 522 female perch heights showed a relatively even distribution over the 0-4 m range of perch height intervals (Fig. 1A). The intersexual comparison of the two distributions was significantly different (Kolmogorov-Smirnov two sample test, $D = 0.355$, $p < 0.01$). However, when the perch height means from individual males ($\bar{x} \pm SE = 2.27 \pm 0.29$ m) was compared with those from individual females ($\bar{x} \pm SE =$

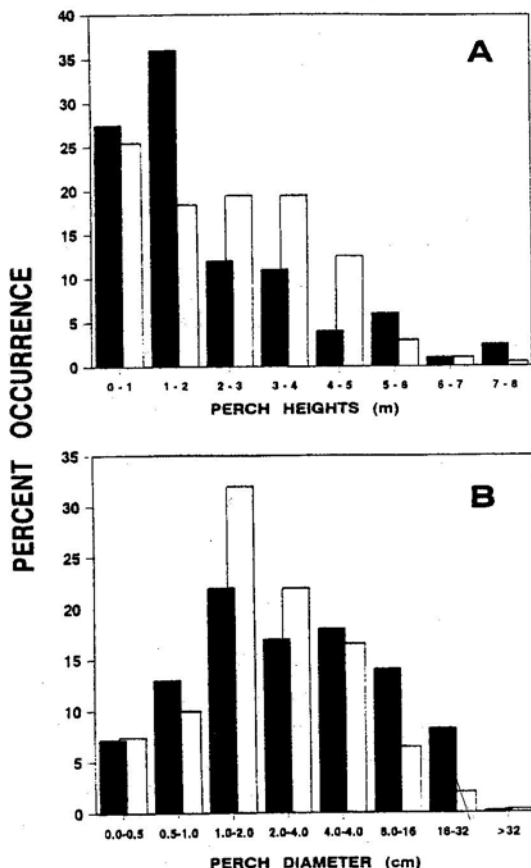


Fig. 1. Distribution of scan samples of perch heights (A) and diameters (B) for 7 adult male (black bars) and 23 females (white bars) *Anolis carolinensis* during May-July in a riparian habitat near Augusta, Georgia.

2.43 ± 0.25 m), no significant difference resulted (Wilcoxon rank sum: $z = -0.86$, $p = 0.87$).

We examined the perch height data for relationships with concomitant seasonal and environmental data. Using a Backward elimination step-wise linear regression model (SAS, 1991), perch heights showed a negative effect due to month of observation and air temperature, but no significant effect due to time of day, relative humidity, and relative cloud cover. Because ambient air temperatures significantly increased with month of observation (May through July; Kruskal-Wallis: $\chi^2 = 151.5$, $p = 0.0001$), it is likely that air temperature was influencing perch heights.

Perch diameter
 The perch diameter distribution of 467 male scan samples was similar to that of 522 female samples, though males tended to use large substrata (e.g. 8.0-32.0 cm diameters) more often than females (Fig. 1B). An intersexual comparison of the perch diameter distribution was significant (Kolmogorov-Smirnov two sample test, $D = 0.770$, $p < 0.01$). The intersexual difference was also significant when comparing mean perch diameters from individual males ($\bar{x} \pm SE = 5.3 \pm 0.57$ cm) with those of individual females ($\bar{x} \pm SE = 3.44 \pm 0.62$ cm; Wilcoxon rank sum: $z = 2.78$, $p = 0.006$). Perch diameter was not significantly correlated with month of observation, air temperature, hour of day, relative humidity, or relative cloud cover (Backward elimination step-wise linear regression, $p > 0.05$).

Home range size (males)

Male home ranges contained 2-6 resident females ($\bar{x} \pm SE = 3.3 \pm 0.57$, Table 1). Based on 851 sets of X, Y, and Z coordinates ($\bar{x} \pm SE = 122 \pm 6.6$ sets/male), home range volumes averaged 69 m^3 (SE 19.9), with mean areas of 51 m^2 (SE 11.1). During the 56 days of continuous observation,

TABLE 1. *Intersexual comparison of size, spatial, and courtship variables for Anolis carolinensis at seven study sites during the breeding season near Augusta, Georgia*

Variable	Males ($N = 7$) mean (standard error)	Females ($N = 23$) mean (standard error)
Snout-vent length (mm)	62.4 (1.31)	50.0 (0.73)
Territory volume (m^3)	69.0 (19.9)	8.3 (1.31)
Number of residents of the opposite sex	3.3 (0.57)	1.0 (0.00)
Territorial overlap (%) with the opposite sex	19 (6.5)	87 (4.2)
Territorial overlap (%) with the same sex	0	18 (4.4)
Frequency of all male-female contacts (per 8 days)	55.0 (6.36)	16.7 (1.99)
Frequency of close male-female contacts (per 8 days)	28.2 (3.26)	8.4 (1.07)
Frequency of copulations per lizard (per 8 days)	5.6 (0.92)	1.7 (0.21)

no male subject shared his home range with another male. However, at three of the study sites we saw a small unmarked male enter the territorial boundary of a marked male, only to be quickly chased out. These 'outside' males were never sighted again, and were not included in the sample of lizards at a study site.

Male home range overlap with resident female home ranges averaged 19% (SE 6.5) by volume and 29% (SE 7.0) by area. The area of combined female home ranges at a study site which fell outside the respective resident male's home range averaged 15%.

Male size (SVL) was significantly correlated with male home range area and volume (Spearman: $r_s = 0.82$, $p = 0.02$; $r_s = 0.79$, $p = 0.04$, respectively) and number of overlapped (resident) females (Spearman: $r_s = 0.78$, $p = 0.04$), but not with the body size of resident females nor the size of female home ranges (Spearman: $r_s = -0.09$, $p = 0.67$; $r_s = 0.37$, $p = 0.11$, respectively).

Home range size (females)

The 23 female home ranges were calculated from 480 sets of X, Y, and Z coordinates ($\bar{x} \pm SE = 21 \pm 0.6$ sets/female). Female home range volume and area averaged 8 m^3 (SE 1.3) and 8 m^2 (SE 1.0), respectively. Unlike males, there were no significant correlations between female SVL and either the area or volume of female home ranges (Spearman: $r_s = 0.17$, $p = 0.47$; $r_s = 0.12$, $p = 0.63$; respectively).

Contiguous female home ranges within study sites overlapped an average of 45% (SE 7.8) by area and 18% (SE 4.4) by volume; the 2.5 fold decrease when area overlap is compared to volumetric overlap indicates that female home ranges were somewhat stacked. Positive correlates to overlap in inter-female home range volumes were size of female home range volumes (Spearman: $r_s = 0.62$, $p = 0.002$) and female movement activity (distance travelled/h, data from Nunez *et al.*, 1997) (Spearman: $r_s = 0.59$, $p = 0.01$).

Courtship behavior

Frequency/duration

During 56 days of observation, 397 male-female encounters occurred (approx. 7/day, Table 1); 198 were distant contacts (type 1), and 199 were close contacts (types 2-4) (Table 2). The frequency with which the four types of

TABLE 2. Frequency of four types of male-female contacts, with their association to receptive females and copulations, by 7 male and 23 female *Anolis carolinensis* at seven study sites during 56 observation days near Augusta, Georgia

Encounter type	Number of contacts	Number of receptive ♀♀	Number of copulations
Type 1 (terminated at distance)	198	0 ¹	0 ²
Type 2 (♂ terminated)	67	67	0
♂ initiated	18	18	0
♀ initiated			
Type 3 (♀ terminated)	61	0	0
♂ initiated	15	0	0
♀ initiated			
Type 4 (led to copulation)	38	38	38
♂ initiated	0	0	0
♀ initiated			

¹ Criterion for receptivity (neck bending) not exhibited at long range.

² Not possible, by definition male and female never touch.

heterosexual contacts occurred was unrelated to a male's SVL, his territory area, or territory volume (General linear model: $df = 3, 384$, $F = 0.01$, $p = 0.998$). Durations of long distance contacts were significantly shorter ($\bar{x} \pm SE = 0.6 \pm 0.04$ min) than of close contacts ($\bar{x} \pm SE = 1.1 \pm 0.08$ min) (Wilcoxon rank sum: $z = -5.44$, $p = 0.0001$). Among the three types of close contacts (types 2-4), there was no significant correlation between type of contact and duration (Spearman: $r_s = 0.09$, $p = 0.21$).

Distant contacts

Distant contacts (type 1) were of low intensity. Both the male and female would observe each other, usually display, but then move away while at a distance. Whether any females of type 1 contacts were sexually receptive could not be determined because the bioassay for receptivity (*i.e.* neck-bend posture by female; Crews, 1973a; Nunez *et al.*, 1997) is only given when the pair is touching or about to touch.

Close contacts

Close contacts (types 2-4) revealed three notable relationships. First, males appeared to differentiate between sexually receptive and non-receptive fe-

males, because during type 2 and 3 contacts males displayed at a significantly lower rate to receptive than to non-receptive females. This relationship was true for both male-initiated contacts, which averaged 4.1 displays/min (± 0.26) to receptive and 5.8 displays/min (± 0.61) to non-receptive females (Wilcoxon rank sum: $z = 1.96$, $p = 0.049$), and for female-initiated contacts, which averaged 2.1/min (± 0.59) to receptive and 5.0/min (± 1.07) to non-receptive females (Wilcoxon rank sum: $z = 2.33$, $p = 0.047$). Second, males bypassed 69% (85/123) of their opportunities to copulate with apparently receptive females (type 2 encounters, Table 2), and, conversely, only 31% (38/123) of encounters with apparently receptive females lead to copulations (type 4 contacts). Third, in those encounters which lead to copulations (type 4 contacts), all were male-initiated contacts (Table 2). Further descriptions of close contacts follow.

Type 2 contacts ($N = 85$), in which by definition the male left the female without copulating, all appeared to involve receptive females (Table 2). In these type 2 contacts, the pairs would exchange displays as they approached, then within touching range, the females would turn their backs toward the males and present their necks. In response, the males declined copulatory neck holds and moved off. In the 18 instances where the females initiated the contact, the males, for whatever reasons, did not appear ready to mate and departed. But in the 67 male-initiated contacts, the departing males had apparently altered their sexual intent during the courtship interval. On an individual male basis, neck-bending resident females were rejected 29 to 91% of the time.

Type 3 Contacts ($N = 76$), in which by definition the female moved away, involved no neck-bending presentations by participating females. Thus, females of type 3 contacts were considered non-receptive and would typically display to approaching males, then run away when approached within approximately 0.5 m. Males sometimes moved after retreating females (23% of instances). However, the general lack of male courtship persistence (Table 2) would indicate that there is little benefit to chasing seemingly unwilling females.

Type 4 Contacts ($N = 38$), in which both sexes were sexually motivated, all involved neck-bending females and were followed by copulation. All type 4 contacts were male-initiated.

In summary, males appeared to distinguish receptive from non-receptive females upon approach (differential display rate), and as a group rejected 85 mating opportunities (69%) with receptive females (type 2 contacts), only copulating when contact was male-initiated. These observations indicate that males are exercising noticeable control over copulatory events.

Inter-male comparisons

Courtship

During their respective 8-day observation periods, individual males engaged in 37 to 81 female contacts ($\bar{x} \pm SE = 55 \pm 6.4$, Table 1) and showed a significant among-male difference (Kruskal-Wallis: $\chi^2 = 22.0$, $df = 6$, $p = 0.001$). We examined the males for correlates between their attributes (body size, territory size), the number and size of their resident females, and their mating performance (courtship and copulation durations and frequencies). The number of contacts with females was most strongly associated with the area of a male's territory (probably reflecting more frequent patrolling activity) and the number of resident females, but was independent of female size and the size of female home range (Table 3). We then re-

TABLE 3. *Results of a general linear model, using partial sums of squares (SAS, 1991) analysis for Anolis carolinensis at seven study sites near Augusta, Georgia*

Dependent variable	Degrees of freedom	F value	p level
<i>Independent variables</i>			
Courtship frequency (male means)	6, 17, 19	8.37	0.001
Male size (SVL)		0.33	0.574
Male territory volume		3.21	0.097
Male territory area		7.81	0.015
Number of resident females		7.89	0.015
Resident female size (SVL)		1.45	0.250
Resident female territory volume		0.95	0.347
Courtship duration (close contacts)	6, 165, 171	3.62	0.002
Male size (SVL)		11.42	0.001
Male territory volume		4.98	0.027
Male territory area		4.71	0.032
Number of resident females		12.73	0.001
Resident female size (SVL)		0.08	0.783
Resident female territory volume		0.23	0.632

moved distant contacts (type 1) from the analysis and focussed on close contacts (types 2-4) because they represent interactions of more immediate biological significance. We found that larger males, who had larger territory volumes, but more resident females (see: Home range size), tended to have fewer close contacts than smaller males (Spearman: $r_s = -0.53$, $p = 0.009$).

Mean durations for close contacts (type 2-4) by individual males ranged from 0.67 to 1.96 min ($\bar{x} \pm SE = 1.01 \pm 0.167$ min), and showed a significant among-male difference (Kruskal-Wallis: $\chi^2 = 16.58$, $df = 6$, $p = 0.011$). Duration of courtship was associated with male size and number of resident females, and like the frequency of courtship, was independent of female size and the size of female home range (Table 3). Thus, larger males, who also tended to have more resident females than smaller males, were associated with the longer bouts of courtship (Spearman: $r_s = 0.15$, $p = 0.034$).

Copulation

Mean copulatory durations for individual males ranged 13-31.5 min ($\bar{x} \pm SE = 22.6 \pm 2.64$ min); the shortest of 38 copulations was 4 min and the longest was 52 min. This inter-male difference was significant (Kruskal-Wallis: $\chi^2 = 14.225$, $p = 0.027$), with copulatory duration positively correlated with male SVL (Spearman: $r_s = 0.358$, $p = 0.02$), and male territory area (Spearman: $r_s = 0.430$, $p = 0.005$), but not correlated with female size (SVL) or number of resident females in a male's territory (Spearman: $r_s = 0.11$, $p = 0.51$ and $r = -0.047$, $p = 0.77$, respectively). Thus, larger males, who also tended to have the largest territories, copulated longer than smaller males.

Male copulatory frequency, without respect to individual females, averaged once every 1.4 days (Table 1), with a range of individual male copulatory rates of once per 1-4 days. This variation among males, however, was not correlated with male and female SVLs, male and female home range volumes, number and duration of courtship contacts, or number of resident females (GLM procedure: $df = 6, 17, 22$, $F = 1.28$, $p = 0.32$). Yet, during the 8-day observation period, the male at each study site copulated at least once with each resident female. Therefore, a male's potential reproductive rate (PRR) was directly related to the number of resident females (and their rate of egg production), and the number

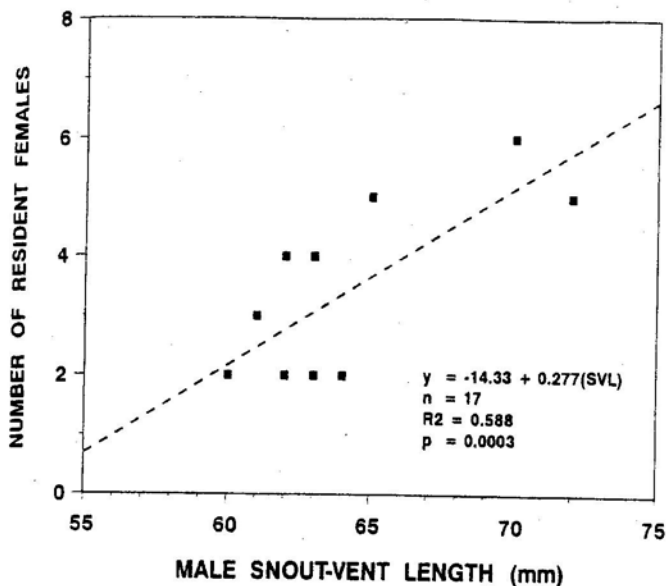


Fig. 2. Number of resident females regressed on corresponding resident male body size at 17 *Anolis carolinensis* study sites near Augusta, Georgia (7 sites from present study; 10 sites from Jenssen *et al.*, 1995b). Some points contain multiple observations.

of resident females in a male's territory was directly related to male SVL (Fig. 2).

Inter-female comparisons

The ovaries of a female *A. carolinensis* alternately ovulate a single ovum, producing a series of single-egg clutches during the breeding season (Smith *et al.*, 1973), which can proceed independently of male presence (Andrews, 1985a). A sexual receptive phase precedes each oviposition (Crews, 1973b), so that the interval between periods of receptivity reflects the inter-clutch interval, and can provide an estimate of a female's rate of egg production (*i.e.* female PRR). Following the field method of Stamps (1975) to estimate the inter-clutch interval, we recorded the days between a female's copulations to represent the interval between receptive periods. An added measure of confidence for our PRR estimate comes from *A. carolinensis* laboratory data which suggest that copulation within a female's

current cycle will inhibit further receptivity until the next cycle (Crews, 1973a).

We found the 23 females averaged 1.6 copulations (SE 0.28) per eight days, or a copulation every 5.0 days. Twelve of these females only copulated once during their observation period, with the longest number of consecutive observation days without mating (including the day of copulation) averaging 5.7 days (SE 0.22, range 5-7 days). But this 5.7 day mean is a truncated estimate of the inter-mating interval because there was not a second mating event for reference. However, the other 11 females copulated twice within their observation periods, averaging 4.4 days (SE 0.47, range 3-7 days) from the day of their first copulation up to, but not including, the day of their second. Thus, there were females with a long estimated clutch cycle (incomplete interval) and those with a short estimated clutch cycle (complete interval). The inter-group difference in estimated cycle duration was significant (Wilcoxon: $z = -2.232$, $p = 0.026$).

The two groups of apparent slow and fast cycling females were not significantly different for SVLs, home range volume, number of neighboring females in their breeding group, or resident male attributes (SVL and territory area and volume) (Wilcoxon tests, z values ranged -0.566 to 0.528 , p values ranged 0.15 to 0.80). Using correlation procedures, only the female SVL variable came close to significance with estimated clutch interval (Spearman: $r_s = -0.386$, $p = 0.069$).

Though we found no evidence for assortative mating among females (*i.e.* no correlates for female PRR), it is possible that an environmental effect may have disrupted a pattern of assortative mating. For example, female anoles can delay oviposition if there is an extended dry period (Stamps, 1976), and egg retention might add confounding variance to our estimated egg-laying intervals. If an environmental effect (*e.g.* drought) were a factor, then all resident females of a study site would share the same effect during their mutual period of observation. However, no significant study site (*i.e.* environmental) effect was found (GLM procedure: $df = 6, 16, 22$, $F = 0.23$, $p = 0.96$). Females within each of the study sites exhibited both short and long cycle estimates.

Discussion

Polygyny: the female response

Anolis carolinensis conforms to the general scheme for polygynous, insectivorous lizards (Stamps, 1983), in which females defend small resource-based territories and males compete to defend as many female home ranges as possible. But from a perspective of sexual selection (e.g. Andersson, 1994), the particular life history and ecological traits of *A. carolinensis* (see Introduction) offer a simple paradigm of reproductive constraints in which to characterize the relative expressions of inter- and intrasexual selection. To begin the characterization, we use the models of polygyny listed in Table 4 as alternative hypotheses for examining the female response within the *A. carolinensis* mating system.

TABLE 4. *Selected models of polygyny, modified from Davies (1991) and Searcy & Yasukawa (1995)*

-
- I. **Male coercion** (males force females to mate polygynously): *expect* evidence of forced copulation, harassment, or intimidation (e.g. Clutton-Brock & Parker, 1995).
- II. **Female choice** (males cannot force females to mate polygynously).
- A. **Cost of polygyny** to females: *expect* inter-female aggression, non-overlapping territories, and a decrease female fitness with more females in a breeding group.
1. **Skewed sex ratio:** *expect* limited number of available males.
 2. **Balanced sex ratio.**
 - a. **Cost uncompensated:** *expect* high female search costs, deceptive males, or maladapted females.
 - b. **Cost compensated:** *expect* high quality male or male resources (e.g. polygyny threshold model; Orians, 1969; Wittenberger, 1976).
- B. **No cost of polygyny** to females: *expect* inter-female tolerance, territorial overlap, and no decrease in female fitness with more females in a breeding group.
1. **Direct benefits:** *expect* increase female fitness with more females in a breeding group (e.g. cooperative female choice; Altmann *et al.*, 1977).
 2. **No direct benefits:** *expect* females to occur randomly in suitable habitat, with no correlation of female fitness to number of females in a breeding group (e.g. neutral-mate-choice model; Lightbody & Weatherhead, 1988).
-

Male coercion model

This model posits that males are able to use force, harassment, or intimidation toward females to secure copulations. No evidence was found to support the coercion model. None of the 38 copulations we observed involved any form of male coercion. In addition, resident males did not employ persistent chases of resident females in any of the 198 type 1 contacts, and it was males who left receptive females in more than half of the close contacts (85 type 2 contacts). Though males were not overpowering females in order to mate, it remains to be seen if floater males, when they are present, might occasionally attempt forced copulations as an alternative mating strategy.

Female choice/cost models

In the cost models of Table 4, female reproduction is restricted by limited (unmated) quality mates, limited mate assistance, and/or scarce resources for optimal female reproduction (e.g. specialized nesting habitat); under these conditions, increasing the number of females in a breeding group should increase inter-female competition, while decreasing female fitness.

The first two 'cost' models of Table 4 are particularly inappropriate for the *A. carolinensis* mating system. *Anolis carolinensis* populations diverge from the 'skewed sex ratio' model by having a 1:1 adult sex ratio (Ruby, 1984; Jenssen *et al.*, 1995a) and males who are reproductive for most or all of the breeding season (Ruby, 1984; Jenssen *et al.*, 1995b; present study). The 'balanced sex ratio'/'uncompensated cost' hypothesis is unsupported as well because female *A. carolinensis* do not incur search costs, being largely sedentary (82% of the day), moving only short distances (≈ 4 m/h), and remaining within relatively small home ranges (8 m³) (Nunez *et al.*, 1997; present study). Additionally, with the absence of parental care and without any appearance of monogamous bonding in the species, males have no need to act deceptively with regard to their mated status.

Cost/compensated

The most likely 'cost' hypothesis to explain the *A. carolinensis* mating system, and the one which has been suggested for *A. carolinensis* (e.g. Crews, 1973c), is the polygyny threshold model (PTM). The PTM proposes that a female's costs of sharing the habitat with other females will be offset if she chooses a high quality male and/or a male in a high quality habitat.

The PTM was developed from, and widely applied to, migratory birds in which males initially entered breeding habitat to compete for optimal territories, then females arrive later to choose among the male-partitioned habitat.

The fit of the 'cost with benefit' paradigm to *A. carolinensis* was unsupported for three important conditions. First, female fitness did not decrease with an increase of females in a breeding group. We found no correlation between the estimated PRR of 23 females and the number of females in their breeding group.

Second, quality of mates and/or habitat did not appear limited or in contention. To begin, the life history and ecological constraints on *A. carolinensis* female reproduction (see Introduction) carry no extraordinary dependency on mate quality (e.g. absence of parental care) or habitat quality (e.g. habitat and dietary generalists), and our results support the same perspective. Regarding mates, we found no evidence of assortative mating when male SVL and territory size were correlated with female SVL, home range size, and PRR. This absence of intersexual correlates is in accord with laboratory-staged, female-choice tests which have revealed no consistent female preference in male traits (e.g. Sigmund, 1983; Andrews, 1985b; review by Tokarz, 1995).

Regarding habitat, females met their needs for mates, food, and shelter within a small volume (8 m³) of habitat. Evidence of inter-female aggression (i.e. defending limited resources) was minimal. We found no correlations among size of female breeding group, female home range size, and female home range overlap. Nunez *et al.* (1997) found only a low incidence of potential territorial behavior by females (movement and display rate of 4 m/h and 14 times/h, respectively), and direct observation of consensual interactions was only once/8 h, in spite of contiguous overlapping home ranges. Although some inter-female aggression occurs (i.e. females are territorial), in comparison with males (Jenssen *et al.*, 1995b), female neighbors are relatively tolerant of one another, supporting the conclusion of Nunez *et al.* (1997) that female habitat requirements are easily met.

Contrary to our perception of inter-female aggression, a recent laboratory study has reached different adaptive inferences. From their observations on captivity-induced female social hierarchies, Andrews & Summers (1996) suggested that the aggression they observed by dominant *A. carolinensis*

females may function adaptively to block the access of subordinate females to males. Conceptually, such a function for female aggression would be unexpected for a species with no male parental care, and it found no empirical support from our field study. Free-ranging females were never seen to guard resident males, and all females were mated at least once within our 8-day observation periods.

Third, a prevailing perception that male and female *A. carolinensis* exhibit asynchronous spring dispersal has created a bias toward *A. carolinensis* as a PTM species. The scenario suggests that males precede females out of winter dormancy by a month (beginning in February), partition the habitat by inter-male contests, and thereby create a mosaic of mate/habitat choices for females who are emerging in March (e.g. Crews, 1973c, p. 165-166). The temporal sequence in which *A. carolinensis* shift from wintering to breeding states definitely needs confirmation, and presently the PTM is not supported by initial field observations. In their November-April study of winter *A. carolinensis* in South Carolina, Jenssen *et al.* (1996) found both male and female *A. carolinensis* to be facultatively active, with almost no consensual aggression occurring at overwintering sites, regardless of month. Dispersal from overwintering sites in South Carolina (based on census data of 130 females and 129 males. J. Congdon, unpubl. data; T. Jenssen, pers. obs.) and in Louisiana (Ruby, 1984) appears to be independent of sex and lasts from March into April. If the latter observations are correct, then adult sexes are simultaneously establishing breeding territories, and female choice will find less opportunity than if the sexes are asynchronously dispersing as suggested by the PTM scenario.

Female choice/no cost models

In these two 'no cost' models (Table 4), female resources should not be critically limited, and intense inter-female aggression would be unexpected. Therefore, an increase in female number to a breeding group should not heighten competition nor lower female fitness. As documented by the preceding arguments, field data best support the 'no cost' models because inter-female aggression was infrequent between neighbors and female PRR did not significantly decrease with size of breeding group. Furthermore, since female PRR was not correlated with breeding group size, the neutral-mate-choice hypothesis (Table 4) best fits our field data.

To fit the criteria for a neutral-mate-choice species, females should settle into breeding home ranges largely independent of each other and largely independent of variation in male quality and territory quality (Lightbody & Weatherhead, 1988). The hypothesis predicts that the reproductive success of females will be independent of 'harem' size (*i.e.* breeding group), and that the territory size of polygynous males will be positively correlated with number of females within a 'harem'. Our data support these predictions, with little evidence for sexual selection among females. Females showed: no significant relationship between their mating success (PRR) and any measured male or female trait (SVL, home range size, number of female neighbors); no correlations between measured female and male traits (*i.e.* assortative mating); and little evidence of inter-female competition for a limited habitat resource (above arguments in 'cost' models). For male PRR, however, male territory size (and male SVL) was positively correlated with number of resident females.

Polygyny: the male response

Without evidence of direct female choice, the distribution of reproductive *A. carolinensis* females in space and time appears to facilitate an intra-sexually selected male response. Females, receptive every 5-6 days over a 4-month breeding season, are distributed in small, contiguous home ranges (Nunez *et al.*, 1997; present study). This pattern of clustered, iteroparous females over a long breeding season creates the conditions in which males engage in territorial contests within an endurance rivalry context. Male PRR is increased by exclusive access to the most females over the longest portion of the 4-month breeding season (Ruby, 1984; present study). The inter-male contests are predictably intense because the *A. carolinensis* polygyny ratio ($\sigma:\text{♀♀}$) of 1:3 (Ruby, 1984; Jenssen *et al.*, 1995b; present study) occurs in populations with a 1:1 adult sex ratio (Ruby, 1984; Jenssen *et al.*, 1995a). This implies that many males have few or no females in their home ranges.

The resulting long-term, intense territorial behavior should cost males, both morphologically and behaviorally. Indeed, in comparison with females, males have an accelerated growth rate (Michaud & Echternacht, 1995) to obtain a large body size (Jenssen *et al.*, 1995a), which is advantageous in inter-male combat, endurance rivalry, and mating opportunities

(e.g. Ruby, 1984; Tokarz, 1985; Leuck, 1995; present study). The endurance component for successful territorial defense produces significant attrition; Ruby (1984) found that 75% of marked resident males had disappeared over a 12 week span of the breeding season. During their residency, males expend much energy and time to conspicuous and risky territorial behavior. Territorial males lose body weight (Ruby, 1984), having the lightest annual body weights during the breeding season (Jenssen *et al.*, 1995a). Compared with females, males exhibit large territories (69 vs 8 m³), no conspecific tolerance (0 vs 18% conspecific home range overlap), much crisscrossing of home range (26 vs 4 m/h), constant displaying throughout the day (107 vs 14 displays/h), and a significant portion of daily activities directed at neighboring conspecifics (10 vs 0.3%) (Jenssen *et al.*, 1995b; Nunez *et al.*, 1997; present study). After the breeding season, the intersexual asymmetries in behavior mostly disappear (Jenssen *et al.*, 1995b, 1996), indicating the extent to which these behavioral dimorphisms are sexually selected.

Besides activities to keep other males away, territorial males should also control mating within their territories, presumably to optimize their fitness with resident females. We found that males influenced courtship and mating events. First, males appeared to recognize at a distance which resident females were receptive (differential display rate, present study). Second, males bypassed 69% of their mating opportunities with receptive females. Though counter-intuitive, this high rejection rate was almost identical as that reported by Jenssen *et al.* (1995b). Third, when males did copulate, the type 4 contact was male-initiated. Fourth, copulatory duration also seemed to be male-influenced. The durations (\bar{x} = 23 min) appeared male-controlled by his mouth hold on the female's neck and his inserted, tumescent hemipenis. Nunez *et al.* (1997) reported that females struggled frequently during the course of copula, even dragging males up to 2 m, without dislodging their mates. We currently speculate that in response to sperm competition (e.g. with 'sneaky' males), resident males may avoid frequent copulations (< 1/day) with resident females to maximize number of sperm in each ejaculate and use long intromission times to influence the effects of sperm precedence (e.g. Stockley, 1997).

Although the *A. carolinensis* mating system may reflect significant intrasexual selection, a consequence of inter-male contests is the opportunity

for indirect female-choice (*sensu* Wiley & Poston, 1996). The extended inter-male contests should present sedentary females with a resident male who has the most stamina, body size, and fighting ability among local males.

References

- Altmann, J. (1974). Observational study of behavior: sampling methods. — *Behaviour* 49, p. 227-267.
- Altmann, S.A., Wagner, S.S. & Lengen-ton, S. (1977). Two models for the evolution of polygamy. — *Behav. Ecol. Sociobiol.* 2, p. 397-410.
- Andersson, M. (1994). *Sexual selection*. — Princeton University Press, Princeton, New Jersey.
- Andrews R.M. (1985a). Oviposition frequency of *Anolis carolinensis*. — *Copeia* 1985, p. 259-262.
- — (1985b). Mate choice by females of the lizard *Anolis carolinensis*. — *J. Herpetol.* 19, p. 284-289.
- Andrews, T.J. & Summers, C.H. (1996). Aggression, and the acquisition and function of social dominance in female *Anolis carolinensis*. — *Behaviour* 133, p. 1265-1279.
- Clutton-Brock, T.H. & Parker, G. (1992). Potential reproductive rates and the operation of sexual selection. — *Quart. Rev. Biol.* 67, p. 437-456.
- — & — — (1995). Sexual coercion in animal societies. — *Anim. Behav.* 49, p. 1345-1365.
- Cockburn, A. (1988). *Social behaviour in fluctuating populations*. — Croom Helm, New York.
- Conant, R. (1975). *Field guide to reptiles and amphibians of eastern and central North America*. — Houghton Mifflin Co., Boston, Massachusetts.
- Crews, D. (1973a). Coition-induced inhibition of sexual receptivity in female lizards (*Anolis carolinensis*). — *Physiol. Behav.* 11, p. 463-468.
- — (1973b). Behavioral correlates to gonadal state in the lizard, *Anolis carolinensis*. — *Horm. Behav.* 4, p. 307-313.
- — (1973c). Social factors associated with the male in the control of reproduction in the female lizard *Anolis carolinensis*: The role of courtship and aggression. — PhD thesis, Rutgers University.
- Davies, N.B. (1991). Mating systems. — In: *Behavioural ecology: an evolutionary approach* (J.R. Krebs & N.B. Davies, eds). Blackwell Scientific Publications, Oxford, p. 263-294.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. — *Science* 197, p. 215-222.
- Fitch, H.S. (1976). Sexual size differences in the mainland anoles. — *Occ. Pap. Mus. Nat. Hist. Univ. Kansas* 50, p. 1-21.
- Fox, W. (1958). Sexual cycle of the male lizard, *Anolis carolinensis*. — *Copeia* 1958, p. 22-29.

- Gordon, R.E. (1956). The biology and biodemography of *Anolis carolinensis*. Voight. — PhD dissertation, Tulane University, New Orleans, Louisiana.
- Hedrick, A.V. & Temeles, E.J. (1989). The evolution of sexual dimorphism in animals: hypotheses and tests. — *Trends Ecol. Evol.* 4, p. 136-139.
- Hollander, M. & Wolfe, D. (1973). Nonparametric statistical methods. — Wiley Press, New York.
- Jenssen, T.A., Congdon, J.D., Fischer, R.U., Estes, R., Kling, D. & Edmands, S. (1995a). Morphological characteristics of the lizard *Anolis carolinensis* from South Carolina. — *Herpetologica* 51, p. 401-411.
- — — — — & Berna, H. (1996). Behavioural, thermal, and metabolic characteristics of a wintering lizard (*Anolis carolinensis*) from South Carolina. — *Funct. Morphol.* 10, p. 201-209.
- — — Greenberg, N. & Hovde, K.A. (1995b). Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. — *Herpetol. Monogr.* 9, p. 41-62.
- — — Hovde, K.A. & Taney, K. (1998). Size-dependent microhabitat use by non-breeding *Anolis carolinensis* lizards. — *Copeia* 1998, p. 774-779.
- King, F.W. (1966). Competition between two south Florida lizards of the genus *Anolis*. — PhD dissertation, University of Miami, Coral Gables, Florida.
- Koenig, W. D. & Albano, S.S. (1986). On the measurement of sexual selection. — *Am. Nat.* 127, p. 403-409.
- Leuck, B.E. (1995). Territorial defense by male green anoles: An experimental test of the roles of residency and resource quality. — *Herpetol. Monogr.* 9, p. 63-74.
- Licht, P. (1973). Influence of temperature and photoperiod on the ovarian cycle in the lizard *Anolis carolinensis*. — *Copeia* 1973, p. 465-472.
- Lightbody, J.P. & Weatherhead, P.J. (1988). Female settling pattern and polygyny: tests of a neutral-mate-choice hypothesis. — *Am. Nat.* 132, p. 20-33.
- Meshaka, W.E., Clouse, R.M., Butterfield, B.P. & Hauge, J.B. (1997). The Cuban anole, *Anolis porcatius*: a new anole established in Florida. — *Herpetol. Rev.* 28, p. 101-102.
- Michaud, E.J. & Echternacht, A.C. (1995). Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. — *J. Herpetol.* 29, p. 86-97.
- Nunez, S.C. (1994). Behavioral, temporal, and spatial relationships in free-ranging female *Anolis carolinensis*. — Thesis, Virginia Tech, Blacksburg, Virginia.
- — — Jenssen, T.A. & Ermland, K. (1997). Female activity profile of a polygynous lizard (*Anolis carolinensis*): Evidence of intersexual asymmetry. — *Behaviour* 134, p. 205-223.
- Orians, G.H. (1969). On the evolution of mating systems in birds and mammals. — *Am. Nat.* 103, p. 589-603.
- Partridge, L. & Endler, J.A. (1987). Life history constraints on sexual selection. — In: *Sexual selection: testing the alternatives* (J.W. Bradbury & M.B. Andersson, eds). Wiley Press, New York, p. 265-277.
- Rose, B. (1982). Lizard home ranges: methodology and functions. — *J. Herpetol.* 16, p. 253-269.
- Ruby, D.E. (1984). Male breeding success and differential access to females in *Anolis carolinensis*. — *Herpetologica* 40, p. 272-280.

- SAS (1991). User's guide: statistics. Release 6.03. — SAS Institute Inc., Cary, North Carolina.
- Searcy, W.A. & Yasukawa, K. (1995). Polygyny and sexual selection in red-winged blackbirds. — Princeton University Press, Princeton, New Jersey.
- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: A review of the evidence. — Quart. Rev. Biol. 64, p. 419-461.
- Sigmund, W.R. (1983). Female preference for *Anolis carolinensis* males as a function of dewlap color and background color. — J. Herpetol. 17, p. 137-143.
- Smith, H.M., Sinelink, G. Fawcett, J.D. & Jones, R.E. (1973). A survey of the chronology of ovulation in anoline lizard genera. — Trans. Kansas Acad. Sci. 75, p. 107-120.
- Stamps, J.A. (1975). Courtship patterns, estrus periods and reproductive condition in a lizard, *Anolis aeneus*. — Physiol. Behav. 14, p. 531-535.
- — (1976). Egg retention, rainfall and egg laying in a tropical lizard *Anolis aeneus*. — Copeia 1976, p. 759-764.
- — (1983). Sexual selection, sexual dimorphism, and territoriality. — In: Lizard ecology: studies of a model organism (R.B. Huey, E.R. Pianka & T.W. Schoener, eds). Harvard University Press, Cambridge, Massachusetts, p. 169-204.
- — (1995). Using growth-based models to study behavioral factors affecting sexual size dimorphism. — Herpetol. Monogr. 9, p. 75-87.
- Stearns, S.C. (1992). The evolution of life histories. — Oxford University Press, New York.
- Stockley, P. (1997). Sexual conflict resulting from adaptations to sperm competition. — Trends Ecol. Evol. 12, p. 154-159.
- Sutherland, W.J. (1996). From individual behaviour to population ecology. — Oxford University Press, New York.
- Tokarz, R.R. (1985). Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). — Anim. Behav. 33, p. 746-753.
- — (1995). Mate choice in lizards: A review. — Herpetol. Monogr. 9, p. 17-40.
- Wiley, R.H. & Poston, J. (1996). Indirect mate choice, competition for mates, and coevolution of the sexes. — Evolution 50, p. 1371-1381.
- Wittenberger, J.F. (1976). The ecological factors selecting for polygyny in altricial birds. — Am. Nat. 110, p. 779-799.