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Field-testing the protandry-based mating system for the lizard, *Anolis carolinensis*: does the model organism have the right model?

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Abstract Using the lizard *Anolis carolinensis* as its subject, an early and enduring model of psychobiology was presented in which neuroendocrines and social behavior interact to coordinate reproduction between the sexes. The adaptive context for the model was protandry, here defined as a “male-first” emergence pattern from winter dormancy to the onset of breeding. In the protandry scenario, males emerge, become reproductive, and contest for territories. Then, pre-reproductive females emerge to settle on male territories, whereby ovarian recrudescence is facilitated by the behavior of courting males. A collateral inference of the protandry sequence is that females are choosing their future mates from among local males and their territories (i.e., intersexual selection). The model and its assumptions, though never validated by field data, have served as the paradigm for many laboratory experiments on *A. carolinensis*. Recently, however, field studies described an intrasexually selected mating system for *A. carolinensis*, without evidence of direct female choice. Differences between the selective inferences from the two perspectives led us to test in the field a number of protandry-based characteristics previously ascribed to *A. carolinensis*. We monitored free-ranging adults across the winter-to-breeding period using data on sex ratios, social behavior, gut contents, sex steroids, and gonadal condition. We found no evidence of protandry, and little support for any of the associated assumptions. Instead, the sexes broadly overlapped in their temporal

transition from winter retreats to an active status in the habitat, with average male reproductive development about 1–2 weeks in advance of females. We replace the traditional protandry-based *A. carolinensis* paradigm with a realistic onset sequence into the breeding season and a new model for the species’ mating system. Our study underscores the need for field validation when laboratory-generated data are fitted to adaptive paradigms.

Keywords *Anolis* lizards · Mate choice · Mating system · Protandry · Sexual selection

Introduction

In an early and enduring model of psychobiology (e.g., Crews 1973, 1975), interacting sequences of neuroendocrine and behavioral events guide the reproductive responses of the lizard, *Anolis carolinensis*. The adaptive context for the proximate mechanisms of the model was patterned on protandry, defined here as a “male-first” emergence pattern from winter dormancy to the onset of breeding (sensu Wirklund and Fagerström 1977). The protandry-based paradigm describes how females optimize ovarian recrudescence and choice of breeding opportunities by emerging after males have established territories (e.g., Crews 1975). Although widely accepted as representing the mating system of *A. carolinensis* (e.g., Drickamer et al. 1996; Alcock 1998), the model was never strictly validated by field data. Recently, several field investigations of *A. carolinensis* (Ruby 1984; Nunez et al. 1997; Jenssen and Nunez 1998) found strong evidence for an intrasexually selected polygynous mating system that features intense intermale competition for access to females throughout an extended breeding season (i.e., endurance rivalry; Andersson 1994). We initiated our study to resolve the discordant views of *A. carolinensis* as a protandric species with opportunities for direct female choice (intersexual selection) and as an endurance rivalry species without direct female choice (intrasexual selection).

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Table 1 Summary of assumptions alluding to adaptive mechanisms inferred by five protandry-based hypotheses

1. Protandry is an *A. carolinensis* trait, with adult males emerging from winter dormancy a month or more before adult females
 - (a) If males emerge before other males (i.e., selection for early males), they are more likely to increase copulation opportunities by securing high-quality territories through consensual contests, and/or by producing more mature spermatozoa before females emerge
 - (b) If females emerge after males (i.e., selection for delayed females), they are less likely to be courted by males who may still be infertile or whose aggressive behavior could disrupt ovarian recrudescence
 - (c) If females emerge after males (i.e., selection for delayed females), they have more opportunity to choose among males and their established territories for the highest-quality mate with the best resources
2. Protandric males initially contest for territories, then shift to predominantly courtship behavior after females emerge
 - (a) If possession of a territory increases mating success, then males controlling territories before female emergence should gain a reproductive advantage over males who do not (i.e., resource-defense polygyny model)
 - (b) If females choose to settle in high- rather than low-quality habitat, then males who emerge before other males are more likely to control the best habitat and should attract more females (i.e., resource-defense polygyny model)
 - (c) If female mate choice is based on the quality of male traits, then males emerging before other males are more likely to exhibit higher-quality traits and should attract more females (male quality is likely to be a correlate of territory quality under the resource-defense polygyny model)
 - (d) If high-quality males and their territories are limited, then competition among females should limit the number of resident females in a male's territory (i.e., polygyny threshold model as a type of resource-defense polygyny)
 - (e) If ovarian recrudescence is affected by male behavior, then females should delay emergence to avoid the negative effects of fighting males, and benefit from the positive effects of courting males (i.e., proximate mechanisms of psychobiology model)
3. Testicular recrudescence is largely completed before female emergence
 - (a) If gonadal recrudescence is accelerated by elevated body temperature during emergence from winter refuges, then males emerging before other males should gain a reproductive advantage, having more time to produce mature spermatozoa before the first females are sexually receptive
4. Testosterone first increases before emergence and then again as mating begins
 - (a) If testosterone mediates activational events, then as a proximate mechanism for protandry, rises in testosterone levels may be expected to initiate the onset of male breeding during the winter (ca December–January) as a prelude to male emergence, gonadal recrudescence, and territorial behavior, and then again after females complete ovarian recrudescence (ca late-April–May) and mating begins
5. Larger males develop protandry-based benefits before smaller males
 - (a) If early male emergence increases mating opportunities, then the more competitive males (i.e., the larger males) should be in a better position, both behaviorally and physiologically, to attract emerging, choosy females sooner than smaller males

The protandry paradigm proposed by Crews (1973) for *A. carolinensis* closely resembles the polygyny threshold model (PTM), which was developed to explain the mating system of many migratory birds (e.g., Verner 1964). In the PTM description for birds, males arrive first in the breeding habitat to compete for territories. Females arrive later to choose breeding sites based on the quality of resident males, their territories, and the possible presence of other females. As a result of potential life-historical and ecological constraints on avian reproduction (e.g., specialized nesting sites, large clutches, homeothermy, altricial young), females incur costs associated with polygyny, such as increased consensual competition for limited resources and reduced male parental assistance. Thus, according to the PTM (e.g., Searcy and Yasukawa 1989), females make mating and nest site choices based on a polygyny threshold (i.e., if costs exceed benefits when settling with a mated male on a high-quality territory with one or more resident females, a female should settle with an unmated male on a lower-quality territory). Essentially, the PTM details a form of resource-defense polygyny, whereby males attract females on the basis of themselves and their resource holdings (Emlen and Oring 1977).

Though not applied as explicitly as for birds, the protandric PTM became the general framework for the *A.*

carolinensis mating system (Crews 1973, 1975), and has subsequently served as the theoretical basis for hypotheses, experimental design, and interpretation of many laboratory studies dealing with the species' behavior (e.g., Crews 1980; Sigmund 1983; Andrews 1985a; Andrews and Summers 1996). As summarized by Crews (1980), the sequence of events for the *A. carolinensis* PTM scenario begins with males emerging from winter dormancy (ca. late January) before females emerge (about early March). In the month or more before female emergence, males undergo gonadal recrudescence, become aggressive, and partition the habitat by means of intense territorial contests. When pre-reproductive females emerge from winter shelters, they find males in established territories, and the previously aggressive males are now interested in courtship. Females then choose their site of residence from among the stable male territories, and ovarian recrudescence begins. After 6–7 weeks (ca. late April to early May), mating and egg laying are initiated.

With the protandry paradigm serving as the adaptive context, Crews (1975, 1980) proposed the following benefits that *A. carolinensis* females would gain by late emergence: avoidance of intermale fighting that is stressful and disruptive to ovarian recrudescence; interaction with currently courting males, whose courtship behavior facilitates ovarian recrudescence, and finding assort-

ative-mating opportunities. Whereas Crews (1980) primarily focused on female reproductive responses to male influences, protandry should have selective advantages for *A. carolinensis* males as well. Studies of non-*Anolis* lizards (e.g., Olsson and Madsen 1996; Olsson et al. 1999) suggest that early emerging males increase their mating success relative to males that emerge later by (1) having more unoccupied high-quality habitat in which to establish a territory, (2) establishing a resident advantage to better defend a desirable territory, (3) having more time to develop mature spermatozoa before females emerge, and (4) accelerating physiological mechanisms that support territorial behavior. Furthermore, larger males who emerged before smaller males would have the benefits from protandry added to their size advantage during intermale contests (e.g., Tokarz 1985).

We identified four hypotheses taken from basic sequence-dependent events summarized from the *A. carolinensis* PTM logic (see Crews 1980, Figs. 2, 28) and a fifth hypothesis as a general prediction for protandry. We used data on adult sex ratios, social behavior, gut contents, sex steroids, and gonadal condition from free-ranging *A. carolinensis* to test the following five hypotheses and their underlying assumptions (Table 1):

1. Protandry is a trait of *A. carolinensis*, with adult males emerging from winter dormancy before (ca 4–6 weeks) adult females due to selection for early male emergence, delayed female emergence, or both.
2. Protandric males exhibit intense territorial behavior before females emerge; after female emergence, males predominantly exhibit courtship behavior.
3. Testicular recrudescence is mostly complete before females emerge.
4. Plasma testosterone of males exhibits a biphasic increase to the onset of breeding, first preceding male emergence and again as mating begins.
5. Larger adult males develop behavioral and physiological capacities to reproduce sooner than smaller adult males.

Methods

The study site was a bottomland hardwood habitat along the Savannah River (Workman and McLeod 1990), located on the Augusta Canal about 12 km northwest of Augusta, Ga., USA (33.3°N, 82°W). Data were collected during four, 3-day collection periods (13–15 February, 13–15 March, 27–29 March, and 24–26 April 1998). Observations took place on sunny days when lizard activity was not affected by inclement weather.

We gathered census data on sex and size classes, body color, and nearest-neighbor distances for lizards observed during site visits. Additional sex and size class data came from census data from a previous study (Jenssen et al. 1996) of overwintering *A. carolinensis* on the Savannah River Site (SRS; 21 km southeast of Augusta Canal). Snout-vent length (SVL) data were divided into the following size classes: 1 (≤ 22 mm), 2 (23–29 mm), 3 (30–39 mm), 4 (40–49 mm), 5 (50–59 mm), 6 (60–69 mm), and 7 (≥ 70 mm). Adult females and males were represented by size classes 4–7 and 5–7, respectively. Body color of lizards, which can shift between brown and green, when initially sighted was ranked 1 if brown or olive, and 2 if green. Body color has no particular relationship with the lizard's immediate-substrate color

(Jenssen et al. 1995), but does reflect sociophysiological states (e.g., Greenberg and Crews 1983). We considered brown to indicate a less active (potential wintering) state and green, a more active state (e.g., Cooper and Greenberg 1992). Relative dispersion, using nearest-neighbor distances, was ranked 1 if a conspecific was within 3 m (i.e., potential aggregated, non-territorial state), or 2 if there were no conspecifics within 3 m (i.e., potential dispersed, territorial state).

Adults, in transition from social tolerance (winter state) to a territorial response (reproductive state), were tested for relative social tendencies with a tethered conspecific placed about 1 m from the subject and left in place for up to 5 min. Response to the tethered lizard was ranked 0 if there was no response, 1 if the subject moved away (aversive response), 2 if the subject approached and displayed (moderate interest), or 3 if the subject attacked (territorial response). Trials resulting in attack were terminated immediately.

Focal observations, of 15-min duration, were made on selected males and females which were subsequently collected to determine endocrine titers, gross gonadal state, and feeding activity (i.e., gut content). We first noted each subject's (1) sex, (2) initial body color, and (3) initial separation distances to nearest neighbors by sex and SVL. Then, during the focal observation period, we recorded the number of (4) feeding attempts, (5) kinds of social interactions and, as indicators of developing territorial behavior and courtship, (6) displays, (7) perch changes, and (8) distance traveled when relocating. If near neighbors were not present to act as a social stimulus during the focal observation period, we introduced a tethered lizard as described above to assay relative aggressive responsiveness. Next, each observed focal lizard was captured and killed to determine its SVL and physiological state. Approximately 200 μ l of blood was drawn for hormone assay, and both the blood sample and its donor were stored on ice in the field. Several hours later, the plasma was centrifuged from the blood sample and transferred along with its donor to dry ice. The plasma and carcasses were kept at -20°C upon return to the laboratory until final analyses.

We measured testosterone (T) in males and progesterone (P) in females. Although estradiol is the primary indicator of female receptivity in *A. carolinensis*, we assayed P because it fluctuates less during the breeding season and is a conservative indicator of clutch production (Jones et al. 1983). Plasma concentrations of T and P were measured by radioimmunoassay (RIA) following methods described in Wingfield and Farner (1975) and Moore (1986). Briefly, samples were equilibrated overnight at 4°C with 2,000 cpm of the appropriate tritiated hormone (Dupont NEN) for individual recovery determinations. Each sample was then extracted twice in 2 ml diethyl ether, and the ether fractions were dried under nitrogen gas and reconstituted in 10% ethyl acetate: 90% isooctane (T) or isooctane pseudosaturated with ethylene glycol (P) (v/v) for chromatographic purification and isolation on Celite (Sigma) columns. The purified eluates were then dried under nitrogen gas, resuspended in assay buffer and equilibrated overnight before RIA. Each steroid was assayed separately using antibodies from Wien Laboratories. We ran standard curves in triplicate and samples in duplicate. Male T samples were randomly assigned and run across two assays, with an interassay coefficient of variation (CV) of 8.1%. Female P samples were run in one assay with an intra-assay CV of 3.8%.

Gonadal condition was evaluated by stage of development and presence of mature gametes. For males, the left testis was weighed (Mettler, type 415) to the nearest 0.1 mg, and the epididymis and adjacent testis tissue examined under a differential interference scope (Leitz, Ortholux II) at $\times 500$ for evidence of mature sperm. Smears of epididymis and testis tissue were ranked 1 if few spermatozoa had tails and none had heads (non-reproductive), 2 if moderate numbers of spermatozoa had tails, but few had mature heads (transitional), or 3 if large numbers of spermatozoa had tails and many had mature, condensed heads (reproductive). The female gonadal condition was evaluated for both ovaries. Using a calibrated ocular on a dissection microscope, we counted and measured ovarian follicles and oviductal yolked and shelled eggs. We

modified the criteria of Licht and Gorman (1970) to rank female recrudescence as 1 if only ovarian follicles <3 mm were present (non-reproductive), 2 if ovarian follicles were beginning to yolk, but still ≤ 5 mm (transitional), or 3 if large (>5 mm) yolked or shelled eggs were present in the oviduct (reproductive).

Feeding activity was estimated by the quantity and distribution of gut contents visible through the translucent walls of the stomach and intestine. Feeding activity was ranked 1 if the digestive tract was empty or there were just a few small food boluses and no stomach contents, or 2 if the intestine contained many large boluses and there were stomach contents. A rank of 1 reflected a non-feeding lizard still associated with its winter retreat, while a rank of 2 reflects a large departure from the wintering state, and suggests that the lizard had dispersed from its winter retreat and acquired a home range.

An indirect estimate of a lizard's activity level was made by adding its feeding activity score to those for its dispersion and body color. Thus, the resulting ordinal activity index (AI) could vary from a minimum of 3 for a non-feeding, aggregated, brown lizard (indicative of a wintering condition) to a maximum of 6 for a feeding, dispersed, green lizard (indicative of a fully active condition).

To test for trends and sample differences, non-parametric procedures (SAS, version 6.12) were used to accommodate continuous and ordinal data without necessity for Gaussian distribution. We primarily wanted to test whether dependent variables changed significantly in response to the four collection periods, categorically ordered 1–4 (February–April). In this application and others where trends in continuous and ordinal variables were of interest, we used either the Spearman correlation procedure or the Mantel-Haenszel χ^2 -test from frequency tables. When performing an analysis of variance within a multivariate model or between two samples, we used the Kruskal-Wallis or the Wilcoxon signed-rank procedures. The α -level for rejecting the null hypothesis was $P \leq 0.05$. However, in cases of multiple test procedures, we used a modified Bonferroni procedure (Hommel 1988) to adjust P -values to avoid making a type I error (i.e., rejecting the null hypothesis when it is true).

Results

Sex ratio and activity index

In census data from two study sites during February–April (total of 434 adults), similar numbers of adult males and females were sighted within each sampling period. Though we saw more males than females during every sampling period, no sex ratio for a sampling period deviated significantly from a 1:1. For the canal study area, the respective numbers of males and females were 9 and 7 for February ($\chi^2=0.25$, $P=0.63$), 24 and 19 for mid March ($\chi^2=0.58$, $P=0.45$), 27 and 17 for late March ($\chi^2=2.27$, $P=0.13$), and 25 and 23 for April ($\chi^2=0.08$, $P=0.77$). For the SRS study site, respective numbers of adult males and females were 30 and 22 for February ($\chi^2=1.23$, $P=0.27$), 69 and 62 for March ($\chi^2=0.37$, $P=0.89$), and 55 and 46 for April ($\chi^2=0.80$, $P=0.41$).

Although both sexes were observed during each collection period, we also used the AI as an estimator for progress between winter quiescence and a fully active status (Fig. 1). The February AI values were near or at minimum (AI=3) for both sexes, indicating that all individuals were inactive and associated with winter retreats. During March, male AI values increased, approaching their maximum (AI=6) in late March. Female AI scores in March in-

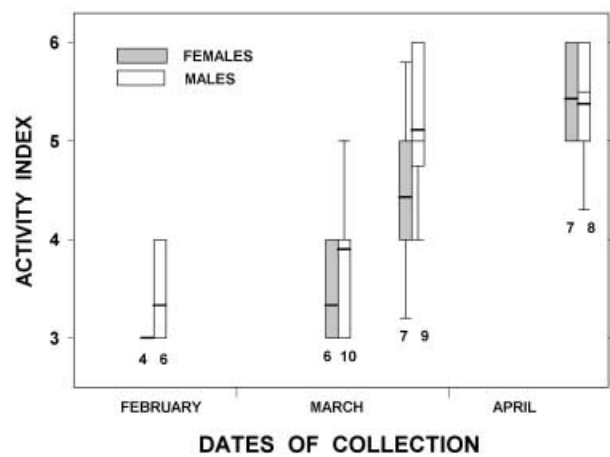


Fig. 1 Box plots of a composite index of three variables (feeding activity, dispersion, and body color) that indirectly reflects activity level for 24 female and 33 male free-ranging *Anolis carolinensis* adults for a sampled population near Augusta, Ga. Ends of boxes give 25th and 75th percentiles, *thick* and *thin* horizontal bars in boxes give the mean and median (which sometimes overlap), respectively, and ends of vertical whiskers give 10th and 90th percentiles, respectively. Sample sizes are given under each bar. Dates of collection are scaled to actual calendar dates

creased more slowly than those of males, lagging by about a week. By mid April, individuals, regardless of sex, exhibited maximum or near-maximum AI values.

The increase in AI values was significantly correlated with the ordered collection periods for both males and females (Spearman coefficient: males, $r=0.77$, $P=0.0001$, $n=33$; females, $r=0.84$, $P=0.0001$, $n=24$). Intersexual comparisons (Bonferroni-adjusted Wilcoxon signed-rank test) of AI values by collection period were not significantly different (mid February: $Z=-1.160$, $P=0.206$, $n=10$; mid March: $Z=-1.485$, $P=0.123$, $n=16$; late March: $Z=-1.391$, $P=0.148$, $n=16$; late-April: $Z=0.000$, $P=1.000$, $n=15$).

Territory-related activity of males

Results of baseline observations of 44 males for territory-related variables (i.e., number of perch changes, distance moved during perch relocations, and display frequency), and then the response of those males in the tether assay, deviated from that predicted by the protandry model. Instead of the expected high initial values for territory-related variables during the first half of the transition period (mid February–mid March), the values were initially low and increased progressively with each subsequent collection period (Fig. 2). Perch change frequency, distance moved between perch changes, and display frequency were significantly and positively correlated with ordered collection periods (Spearman correlation, $r=0.535$, $P=0.0002$; $r=0.646$, $P=0.0001$; $r=0.630$, $P=0.0001$). Only April values for these three variables approached the levels observed for breeding males by Jenssen et al. (1995).

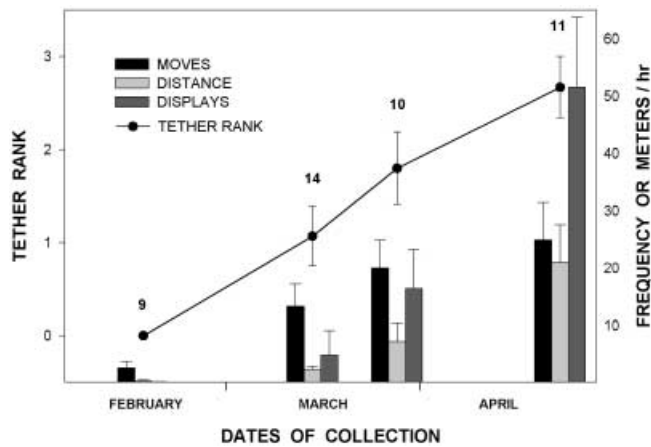


Fig. 2 Mean number of moves, distance traveled (m), and number of displays per hour from focal observations for 44 free-ranging male *A. carolinensis* adults indicated by bars, and the tether index scores of the same males toward a tethered conspecific (connected dots), where 0 is no response, 1 is withdrawal, 2 is approach, and 3 is attack. SEs of all means are shown by vertical whiskers. Sample sizes are given over each collection period. Dates of collection are scaled to actual calendar dates

Ranked responses of males to the tether assay for aggressiveness also gradually increased with subsequent collection periods (Mantel-Haenszel $\chi^2=10.54$, $P=0.001$). However, the attack response (indicative of a territorial male) had only developed in males of the April collection period (Fig. 2) when females were already reproductive (Fig. 3A). We also examined a larger dataset ($n=64$) that included 22 additional males for which there were no concomitant focal observations. Mean tether ranks for the four collection periods reflected values similar to those in Fig. 2 (February: 0.0, no response; mid March: 1.1, aversive response; late March: 1.9, interested response; April: 2.8, attack response) and there was also a significant increase with collection period (Mantel-Haenszel $\chi^2=31.68$, $P=0.001$).

Heterosexual approaches (i.e., possible courtship) during 7.5 h of focal observations on 30 females were observed in only one instance in the April sample, resulting in no significant correlation with order of collection periods (Kruskal-Wallis, $\chi^2=2.750$, $P=0.432$). During 11 h of focal observations on 44 males, no male approached a female in February ($n=9$) or late March ($n=14$); 1 did so in mid March ($n=10$), and 4 in April ($n=11$); the occurrence of approaches was not significantly correlated with collection periods (Kruskal-Wallis, $\chi^2=8.75$, $P=0.099$).

Gonadal development

Contrary to the protandry prediction that male gametogenesis would reach completion in the first half of the transition period (ca mid-February–mid March), testicular recrudescence was only beginning by mid March

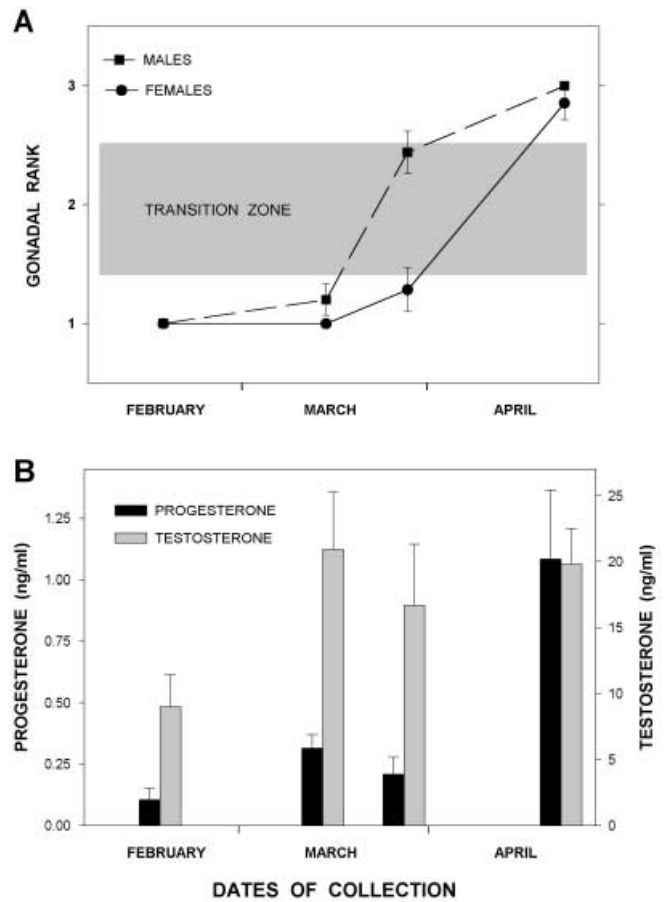


Fig. 3 **A** Means and SEs of gonadal ranking for 24 female (dashed line) and 33 male (solid line) free-ranging *A. carolinensis* adults, where 1 is no criteria, 2 is transitional criteria, and 3 is full criteria for oviductal eggs or epididymal spermatozoa (see Methods for criteria). **B** Means and SEs of plasma progesterone from 24 female, and testosterone from 33 male free-ranging *A. carolinensis* adults. Sample sizes are the same as given in Fig. 1. Dates of collection are scaled to actual calendar dates

(Fig. 3A), when females were already active in the habitat (Fig. 1). Of the nine males examined in late March, four were still transitional (rank 2), while the remaining had epididymal spermatozoa (rank 3). By the April sample, all males were ranked as reproductive. Gametic development was also significantly correlated with testicular mass (i.e., left testis; Spearman correlation, $r=0.77$, $P=0.0001$, $n=33$) which averaged 11.8 ± 0.98 (SE) mg in February ($n=6$), 15.0 ± 1.78 mg in mid March ($n=10$), 21.4 ± 1.99 mg in late March ($n=9$), and 38.5 ± 3.28 mg in late April ($n=8$).

Female gametogenesis progressed more slowly than male reproductive development. No females contained oviductal eggs during March, but some were initiating gametic development by late March (Fig. 3A). In the late-March sample, five females had no follicular enlargement (rank 1), and two females did (rank 2). In the April sample, however, all but one of the females had commenced egg laying and contained shelled oviductal eggs (rank 3). For both males and females, gametic de-

Table 2 Sample sizes (n), Spearman Correlation coefficients (r), and probabilities (P and adjusted P for multiple test) for 12 dependent variables using snout-vent length as the independent variable for adult male *Anolis carolinensis* during the February–April transition period

Variable	n	r	P	Adjusted P
Distribution (aggregated→dispersed)	85	0.043	0.693	0.995
Skin color (brown→green)	85	0.150	0.171	0.513
Feeding activity from gut content (none→frequent)	33	0.294	0.082	0.328
Moves during focal observations (none→many)	44	0.215	0.161	0.483
Distance moved during focal observations (none→far)	44	0.339	0.024	0.192
Displays during focal observations (none→many)	44	0.571	0.0001	0.0012
Response level to tethered male (none→attack)	64	0.309	0.013	0.108
Aggressive bouts during focal observations (none→many)	44	0.001	0.995	0.995
Courtship bouts during focal observations (none→many)	44	0.353	0.019	0.152
Plasma testosterone concentration (low→high)	33	0.295	0.096	0.342
Testis weight (light→heavy)	33	0.499	0.002	0.022
Gonadal development (little→well-developed)	33	0.303	0.073	0.292

velopment was progressive and positively correlated with ranked collection periods (Spearman correlation, $r=0.90$, $P=0.0001$, $n=33$; $r=0.83$, $P=0.0001$, $n=24$, respectively), and gametic development did not differ between the sexes, except for late March, when male gametic stage was advanced relative to that of females (Wilcoxon signed-rank test, $Z=-2.945$, $P=0.003$, $n=16$).

Endocrine titers

Male plasma T concentrations did not oscillate in a biphasic pattern as suggested by the protandry model, but rather made a single mid-March increase (Fig. 3B). Plasma T was lowest in the February sample (mean=9.0 ng/ml), highest (mean=20.9 ng/ml) in mid-March, and remained high in the late-March and April samples. Because of the single large increase in plasma T during the first half of the transition period, T did not correlate with ranked collecting periods (Spearman correlation, $r=0.28$, $P=0.104$, $n=33$), nor did a male's plasma T concentration correlate with either his stage of gametic development (Spearman correlation, $r=0.24$, $P=0.171$, $n=33$) or testicular mass (Spearman correlation, $r=0.25$, $P=0.158$, $n=33$).

In comparison with male plasma T, female P was significantly correlated with ranked collection periods (Spearman correlation, $r=0.74$, $P=0.0006$, $n=24$). From a mid-February low (mean=0.11 ng/ml), P increased sharply with the late-April sample (mean=1.08 ng/ml) (Fig. 3B). Because P is correlated with egg laying, the association of elevated P with only April females is not surprising, because they were the first sampled individuals who had begun laying clutches (Fig. 3A).

Large-male advantage

Contrary to the last protandry prediction, larger adult males did not emerge before smaller adult males. Instead, the mean SVL of sampled adult males (i.e., >50 mm SVL) tended to increase slightly from collection periods 1 through 4, being 57.7 mm (SE 2.43, $n=9$), 58.0 mm (SE 1.00, $n=24$), 58.3 mm (SE 1.10, $n=27$), and

60.5 mm (SE 0.79, $n=25$), respectively. In addition, we tested the 12 variables listed in Table 2, both within and between collection periods, for a significant relationship with SVL. Within each of the four collection periods, the Spearman correlation procedure revealed that no variable correlate significantly with SVL, except testis mass of the April sample ($r=0.783$, $P=0.022$, $n=8$). Nor was SVL significantly correlated with any variable when the first two collection periods were pooled (i.e., first half of transition period). If larger males were selected to advance their reproductive opportunities sooner than smaller males, we would expect relevant variables during the February or mid-March collection periods to correlate with SVL. But there was no evidence for such a trend.

Two significant relationships with SVL, unrelated to protandry, were apparent when the temporal sequence was removed by pooling the adult male data from all collecting periods (Table 2). Of the 12 tested variables, Spearman correlations were significant for increasing body size with increasing rate of display and testis mass.

Profile of transition period

A profile of the male and female response to the February–April transition period was constructed from 12 variables (Table 3). Using ordered collection periods as the independent variable, a Kruskal-Wallis procedure was run separately on adult male and female data (Table 3) to indicate the extent to which each variable changed progressively during the transition period. Both sexes showed significant increases for nearest-neighbor distance (i.e., dispersion), brown to green body color (i.e., sociophysiological arousal), gut contents (i.e., feeding activity), and developing gonadal recrudescence (Table 3). Of the variables that were sex specific, female P titers and male gonad weight also increased significantly with collection period, but male T titers did not.

The territory indicators in Table 3, however, suggested a sex bias. Three variables associated with territorial patrol and advertisement (i.e., number of moves, movement distance, and display number) significantly increased with collection dates for males, but not females

Table 3 Sample sizes (n), test statistic (χ^2), and probabilities (P and adjusted P for multiple tests) for 12 dependent variables of a Kruskal–Wallis analysis of variance, with collection period as the independent variable for adult *A. carolinensis* during the February–April transition period

Variable	Male				Female			
	n	χ^2	P	Adjusted P	n	χ^2	P	Adjusted P
Skin color	85	24.83	0.0001	0.0007	66	28.31	0.0001	0.0008
Dispersion	85	20.41	0.0001	0.0007	66	20.42	0.0001	0.0008
Feeding activity	33	27.26	0.0001	0.0007	24	19.27	0.0002	0.0014
Tether response	64	34.20	0.0001	0.0007	33	9.61	0.022	0.11
Movement number	44	13.23	0.004	0.016	30	6.13	0.106	0.424
Movement distance	44	18.94	0.0003	0.0015	30	3.90	0.272	0.432
Display number	44	17.67	0.0005	0.0025	30	2.75	0.432	0.432
Aggressive bouts	44	3.94	0.268	0.268	30	0.0	–	–
Courtship bouts	44	8.75	0.033	0.099	30	2.75	0.432	0.432
Testis mass	33	24.00	0.0001	0.0007	–	–	–	–
Testosterone	33	6.62	0.085	0.17	–	–	–	–
Gonadal development	33	30.44	0.0001	0.0007	24	19.40	0.0002	0.0014
Progesterone	–	–	–	–	24	14.86	0.002	0.012

(Table 3, Fig. 2). A fourth variable, tether response, tracked relative intolerance of conspecifics as an indicator of territorial defense. Tether response scores also increased significantly with collection period for males, but not females (Table 3), concluding in April with an average of 2.8 (attack response) for males. In contrast, females, the less territorial sex during the breeding season, had average scores of 0.38, 0.63, and 0.64 (non-responsive to aversive) for February, mid March, and late March, respectively, and concluded with an April average of 1.8 (moderate interest).

Finally, from 15-min focal observations, neither sex showed a significant increase with collection dates for naturally occurring bouts of conspecific interactions (5 instances by 44 observed males and 0 instances by 30 observed females) or heterosexual interactions (5 instances by 44 observed males and 1 instance by 30 observed females) (Table 3). Observed interactions were limited to displaying and/or approaching, with no occurrences of actual fighting or copulations. In 18.5 h of observations during the transition period, social encounters of any kind were infrequent (less than once/1.5 h).

Discussion

Absence of protandry

Our study, the first to test the protandry paradigm for *A. carolinensis* under field conditions, found little or no support for five protandry-based hypotheses (see Introduction, Table 1). The principal hypothesis that protandry is a trait of *A. carolinensis*, with adult males emerging a month or more before adult females, was not supported by either adult sex ratios or the AI. Beginning in the winter, males and females of all size classes aggregate at winter retreats and facultatively bask on sunny days; during these short periods of emergence, the lizards are brown and almost never move, feed, or interact socially (Jenssen et al. 1996; present study). Then, in March, with the sex ratio and AI data showing no signif-

icant intersexual differences within any collection date, males and females leave their winter refugia and disperse into home ranges in the local habitat. Though average male AI values were higher than average female AI scores for respective March collection dates, the broad variance around the AI averages (Fig. 1) indicates that the transition between lizards in a wintering state to lizards that are dispersed, feeding, and green is not a tightly timed event in the population, nor is the sequence strongly sex biased. Rejection of the protandry hypothesis renders its underlying assumptions largely inappropriate for *A. carolinensis* (see Table 1). Furthermore, the remaining four protandry-based hypotheses and their assumptions also become questionable, and need to be examined.

The two hypotheses predicting that males during the first half of the transition period (i.e., before female emergence) should be both intensely territorial and reproductive were rejected. Instead, both male territory-related behavior (Fig. 2) and spermatogenesis (Fig. 3A) developed gradually across the March transition period. Except for T, mid-March males had not reached breeding levels for any variable. By late March, when some sampled females had begun ovarian recrudescence, about half the sampled males were not yet reproductive and all male territorial indicators were still below breeding levels. These field data challenge previous assumptions (see Table 1) for the species' mating system, mate choice strategies, mode of selection, and proximate mechanisms of reproduction.

With regard to mating system, mate choice, and mode of selection, the absence of protandry eliminates the opportunity for females to choose a breeding site from among established territories of reproductively active males, and reduces the opportunity for the intersexual selection that is inferred within a protandry-based mating system (e.g., PTM). We found males and females more or less synchronously entering the habitat before either sex had developed a territorial response, initiated gonadal recrudescence, or begun courtship (Figs. 2, 3). Because March females had settled into the

habitat in the presence of sexually inactive males, it is difficult to envision an intersexual selection mechanism whereby females make mate and site decisions based on male courtship behavior or male resources gained through intermale contests. We conclude that females do not incur a fitness cost by synchronously emerging with males and, conversely, neither sex appears selected for the advantages attributed to protandric emergence (see Table 1).

Field data also bring into question the relevance of the proximate mechanisms underlying the protandry-based psychobiology model of *A. carolinensis* (*sensu* Crews 1980). First, the laboratory protocol (Crews 1973) that produced male-induced inhibition and stimulation of ovarian development used significant social compression by reducing spatial relationships and extending temporal proximity beyond that normally experienced by free-ranging *A. carolinensis*. Spatially, the cages (<0.2 m³) that held 30 females and 1–5 males were 1/1,200–1/1,700 the normal volume of habitat occupied by this combination of free-ranging females and males (8 m³/female and 69 m³/male; Jenssen and Nunez 1998). Temporally, the continuous 6-week duration of the heterosexual experiments was >2,400-fold that of voluntary heterosexual contacts, where a territorial male and a resident female average less than 5 min/day in close proximity, excluding a copulation once every 5 days (Nunez et al. 1997; Jenssen and Nunez 1998). The large departures in laboratory treatment and control conditions from the natural state may, in themselves, produce significant physiological and behavioral responses (e.g., Moore et al. 1991; Lambrechts et al. 1999).

Second, the absence of field data supporting protandry seriously diminishes the selective context for the protandry-based model that Crews (1980) suggested for *A. carolinensis*. The laboratory-generated effects of inhibition and stimulation of ovarian recrudescence by aggressive and courting males, respectively, are arguably adaptive (i.e., proximate mechanisms) if placed in a protandry context. Thus, the psychobiology model specified that (1) females should emerge late to avoid males who were previously contesting and aggressively signaling over territories and, in so doing, late-emerging females would not incur a reproductive penalty from the inhibitory effects of intense male territorial behavior, and (2) if females emerged after males had established their territories, then these late-emerging females would have a reproductive advantage from the stimulation effects of courting males who now had stable territories and contested less.

Field observations, however, did not find the social sequences or intensities required of either proximate mechanism. With regard to the inhibition effect of aggressive males, not only did male and female *A. carolinensis* disperse from overwintering sites together, but there was no male-generated aggression during the first half of the transition period (mid February–mid March) that females should avoid as proposed in the psychobiology model. Instead, male territorial indicators gradually

increased over the transition period. Even by late March when some females were initiating ovarian recrudescence, male territorial indicators were significantly increasing, but still below breeding levels. For example, late-March males averaged one-fifth the baseline display rate (20/h) of fully territorial males (>100/h; Jenssen et al. 1995), moved one-third the distance (8 m/h) of fully territorial males (27 m/h; Jenssen et al. 1995), and most did not attack tethered conspecifics. With both ovarian recrudescence and male territory indicators increasing together, the field evidence rejected the proposition that male aggressive behavior exerts a selected inhibitory effect on female reproductive development.

With regard to the stimulation effect of courting males, we found little evidence for prominent levels of courtship in the second half of the transition period (late March–April) by which ovarian recrudescence should be advanced as proposed in the psychobiology model. Male-female interactions were infrequent (Table 3), and during the late March–April collection dates when females exhibited all stages of ovarian development, we observed only one late-March and four April contacts in 9.5 h of focal observations. Even during the breeding season, territorial males infrequently court resident females (twice a day/female, Jenssen and Nunez 1998), and then for brief durations (\approx 1.1 min/encounter; Jenssen and Nunez 1998). These field data do not invalidate courting males as an excitatory stimulus for ovarian recrudescence, but they do question the extent to which female fitness would be enhanced. Attainment of reproductive condition by females does not require the presence of a male. Egg laying is initiated by cues from photoperiod and environmental temperature, even in the absence of males (Licht 1973; personal observation). Nevertheless, there remains the still untested prospect that free-ranging males may facilitate a small temporal advance to ovarian recrudescence.

A third proximate mechanism suggested by the protandry model (see Crews 1980, Fig. 28) is a biphasic increase in male plasma T, with the first T increase coming before male emergence, testicular recrudescence, and territorial behavior, and the second occurring with the start of courtship and mating after emerged females have become sexually receptive. We found a simpler pattern. Plasma T increased only once (by mid March), after males began dispersing from winter refugia, and was concurrent with the initial increases in territory-related behaviors, spermatogenesis, and testicular hypertrophy. Plasma T then remained at increased levels into the mating season, and was not closely coupled with increasing levels of male reproductive variables. In Florida, Tokarz et al. (1998) also reported a single increase of plasma T in *A. sagrei*, an anole with a pattern of mating behavior similar to that of *A. carolinensis* (Nunez et al. 1997; Jenssen and Nunez 1998; Tokarz 1998). The T levels of *A. sagrei* were even more uncoupled from behavioral and gonadal variables than we found for transitional *A. carolinensis*.

Our findings also cause rejection of the last hypothesis that larger males should develop the behavioral and physiological capacity to reproduce sooner than smaller males. If the transition period is reproductively advantageous for males (i.e., selection for early male emergence), then large, competitive males (e.g., Tokarz 1985) might be expected to develop the behavioral and physiological mechanisms that enhance reproductive potential in advance of smaller males. However, body size (SVL) was not significantly correlated with any behavioral variables (e.g., feeding activity, tether rank, display rate, distance moved, or number of aggressive and courtship bouts) or physiological variables (plasma T and gonadal development) during any of the collection periods.

The *A. carolinensis* mating system

Females should optimize their reproductive response within the limits of their life history and ecological traits (e.g., Partridge and Endler 1987; Stearns 1992; Sutherland 1996). Then, within the temporal and spatial distribution of reproductive females, males should optimize their reproductive response (e.g., Emlen and Oring 1977; Cockburn 1988; Davies 1991). For female *A. carolinensis*, an initial life history constraint is a single-egg clutch (Smith et al. 1973). As a consequence of clutch size limitation, female reproductive success depends on the duration of the breeding season and the frequency with which a female can repeat clutch laying. Temporally, a female is reproductive for approximately 4 months (e.g., Ruby 1984; Jenssen and Nunez 1998), laying one egg at about weekly intervals (Andrews 1985b; Jenssen and Nunez 1998). Spatially, breeding females are found in stable, small, and overlapping home ranges with conspecific neighbors that are relatively tolerant of one another (Nunez et al. 1997; Jenssen and Nunez 1998).

Because male fitness is independent of any parental care, male *A. carolinensis* increase their reproductive success by attempting to mate with multiple females who are sedentary, closely spaced, and reproductive over a long breeding season. In a version of female-defense polygyny (sensu Emlen and Oring 1977), males use intense territorial behavior to exclude other males from as many females as possible (Ruby 1984; Jenssen et al. 1995; Jenssen and Nunez 1998). The long breeding season extends intermale competition for matings into an endurance rivalry. The intensity of the endurance-rivalry is reflected by a 1 male:3 female polygyny ratio within a population that has a 1:1 operational sex ratio (Ruby 1984; Jenssen et al. 1995; Jenssen and Nunez 1998). The *A. carolinensis* mating system appears to be the result of intrasexual selection, with no obvious evidence of direct female choice (Ruby 1984; Jenssen and Nunez 1998); this may be why previous attempts to explore mechanisms of female choice in *A. carolinensis* have been equivocal (reviewed by Tokarz 1995).

A new model

Our study documented that pre-reproductive males and females move concurrently from overwintering shelters onto home ranges in advance of breeding responses. There is no apparent selection for females to choose among the best resources being controlled by the most competitive males (i.e., no evidence for intersexual selection or resource-defense polygyny). Why females settle where they do is an open question, but it does not seem to be primarily influenced by male-based choices. Field data for other lizard species seem to support a similar conclusion (e.g., M'Closkey et al. 1987; Hews 1993; Tokarz 1998). What, then, are the most likely origins of the intensely patrolled male territories that contain multiple female residents? Rather than females moving to join established males, we suggest the reverse. By the end of the transition period (late March–early April), males are completing gametogenesis 1–3 weeks before females (Fig. 3A). Likewise, sexual behavior should develop in males before females, and motivate males to seek out females. By this logic, males should be attracted to local habitat that already contains established females. With initial contests and subsequent threats, each of the most competitive males would partition the habitat in which the females reside to defend as many females as possible. Relative male success for controlling access to multiple mates would depend on the density of females and the aggressive pressure from adjacent males.

In our scenario, male fitness is modeled on female-defense polygyny (sensu Emlen and Oring 1977), in which the potential reproductive rate of male *A. carolinensis* is positively correlated with male body size, size of male territory, number of resident females, and duration on his territory (Ruby 1984; Jenssen and Nunez 1998). To model female fitness within polygyny, we dismiss a PTM-based mating system and suggest a “neutral mate choice” model (sensu Lightbody and Weatherhead 1988) as best fitting the field data for *A. carolinensis* females. The neutral mate choice model is a “no cost” model for females of polygynous species where conspecific competition is low because female reproductive requirements are easily met (Searcy and Yasukawa 1989). As predicted by the neutral mate choice model, female *A. carolinensis* when entering typical habitat should settle into home ranges with minimal differential response to either one another or to variations in mate/habitat quality.

Three lines of field evidence from *A. carolinensis* support the criteria for the neutral mate choice model. First, *A. carolinensis* females are insectivorous and habitat generalists without parental care; thus, they meet their resource requirements (i.e., food, shelter, and mates) in small home ranges ($\approx 8 \text{ m}^3$) with little competition between conspecific neighbors ($\approx 20\%$ home range overlap, aggressive interactions once/8 h; Nunez et al. 1997). Second, no variable measured for groups of breeding *A. carolinensis* provided evidence of assortative mating or costs to female reproductive success due to polygyny

(Jenssen and Nunez 1998). Third, the present study indicates that *A. carolinensis* females establish their home ranges before either sex is reproductively active, thus diminishing the likelihood that females use male-related criteria in their selection process. As reproductive activity begins, females are closely spaced and sedentary, a condition that promotes passive mate selection (i.e., indirect female choice; sensu Wiley and Poston 1996), whereby spatially grouped females will attract the defense and matings from males with the most stamina, largest body size, and greatest fighting ability.

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References

- Alcock J (1998) Animal behavior, 6th edn. Sinauer, Sunderland, Mass
- Andersson M (1994) Sexual selection. Princeton University Press., Princeton, NJ
- Andrews RM (1985a) Mate choice by females of the lizard, *Anolis carolinensis*. *J Herpetol* 19:284–289
- Andrews RM (1985b) Oviposition frequency of *Anolis carolinensis*. *Copeia* 1985:259–262
- Andrews TJ, Summers CH (1996) Aggression, and the acquisition and function of social dominance in female *Anolis carolinensis*. *Behaviour* 133:1265–1279
- Cockburn A (1988) Social behaviour in fluctuating populations. Croom Helm, New York
- Cooper WE, Greenberg N (1992) Reptilian coloration and behavior. In: Gans C, Crews D (eds) Biology of the Reptilia, vol 18. Physiology E: hormones, brain, and behavior. University of Chicago Press, Chicago, pp 298–422
- Crews D (1973) Social factors associated with the male in the control of reproduction in the female lizard *Anolis carolinensis*: the role of courtship and aggression. Ph.D thesis, Rutgers University
- Crews D (1975) Psychobiology of reptilian reproduction. *Science* 189:1059–1065
- Crews D (1980) Interrelationships among ecological, behavioral, and neuroendocrine processes in the reproductive cycle of *Anolis carolinensis* and other reptiles. In: Rosenblatt JS, Hinde RA, Beer C, Busnel M (eds) Advances in the study of behavior, vol 11. Academic Press, New York, pp 1–74
- Davies NB (1991) Mating systems. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 263–294
- Drickamer L, Vessey S, Meikle D (1996) Animal behavior, 4th edn. Brown, Dubuque, Iowa
- Emlen S, Oring L (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Greenberg N, Crews D (1983) Physiological ethology of aggression in amphibians and reptiles. In: Svare BB (ed) Hormones and aggressive behavior, Plenum, NY, pp 469–506
- Hews DK (1993) Food resources affect female distribution and male mating opportunities in the iguanian lizard *Uta palmeri*. *Anim Behav* 46:279–291
- Hommel G (1988) A stagewise rejective multiple test procedure based on a modified Bonferroni test. *Biometrika* 75:383–386
- Jenssen TA, Nunez SC (1998) Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. *Behaviour* 135:981–1003
- Jenssen TA, Greenberg N, Hovde K (1995) Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetol Monogr* 9:41–62
- Jenssen TA, Congdon JD, Fischer RU, Estes R, Kling D, Edmands S, Berna H (1996) Behavioral, thermal, and metabolic characteristics of a wintering lizard (*Anolis carolinensis*) from South Carolina. *Funct Ecol* 10:201–209
- Jones RE, Guillette LJ Jr, Summers CH, Tokarz RR, Crews D (1983) The relationship among ovarian condition, steroid hormones, and estrous behavior in *Anolis carolinensis*. *J Exp Zool* 227:145–154
- Lambrechts MM, Perret P, Maistre M, Blondel J (1999) Do experiments with captive non-domesticated animals make sense without population field studies? A case study with blue-tits' breeding time. *Proc R Soc Lond B* 266:1311–1315
- Licht P (1973) Influence of temperature and photoperiod on the annual ovarian cycle in the lizard *Anolis carolinensis*. *Copeia* 1973:465–472
- Licht P, Gorman GC (1970) Reproductive and fat cycles in Caribbean *Anolis* lizards. *Univ Calif Publ Zool* 35:1–52
- Lightbody KP, Weatherhead PJ (1988) Female settling patterns and polygyny: tests of a neutral-mate-choice hypothesis. *Am Nat* 132:20–33
- M'Closkey RT, Baia KA, Russell RW (1987) Tree lizard (*Urosaurus ornatus*) territories: experimental perturbation of the sex ratio. *Ecology* 68:2059–2062
- Moore MC (1986) Elevated testosterone levels during nonbreeding-season territoriality in a fall-breeding lizard, *Sceloporus jarrovi*. *J Comp Physiol A* 158:159–163
- Moore MC, Thompson CW, Marler CA (1991) Reciprocal changes in corticosterone and testosterone levels following acute and chronic handling stress in the tree lizard *Urosaurus ornatus*. *Gen Comp Endocrinol* 81:217–226
- Nunez SC, Jenssen TA, Ersland K (1997) Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour* 134:205–223
- Olsson MT, Madsen T (1996) Costs of mating with infertile males selects for late emergence in female sand lizards. *Copeia* 1996:462–464
- Olsson MT, Birkhead T, Shine R (1999) Can relaxed time constraints on sperm production eliminate protandry in an ectotherm? *Biol J Linn Soc* 66:159–170
- Partridge L, Endler JA (1987) Life history constraints on sexual selection. In: Bradbury JW, Andersson MB (eds) Sexual selection: testing the alternatives. Wiley, New York, pp 267–277
- Ruby DE (1984) Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* 40:272–280
- Searcy WA, Yasukawa K (1989) Alternative models of territorial polygyny in birds. *Am Nat* 134:323–343
- Sigmund WR (1983) Female preference for *Anolis carolinensis* males as a function of dewlap color and background color. *J Herpetol* 17:137–143
- Smith HM, Sinelink G, Fawcett JD, Jones RE (1973) A survey of the chronology of ovulation in anoline lizard genera. *Trans Kans Acad Sci* 75:107–120
- Stearns CS (1992) The evolution of life histories. Oxford University Press, Oxford
- Sutherland WJ (1996) From individual behaviour to population ecology. Oxford University Press, Oxford
- Tokarz RR (1985) Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Anim Behav* 33:746–753
- Tokarz RR (1995) Mate choice in lizards: a review. *Herpetol Monogr* 9:17–40

- Tokarz RR (1998) Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. *Herpetologica* 54:388–394
- Tokarz RR, McMann S, Seitz L, John-Alder H (1998) Plasma corticosterone and testosterone levels during the annual reproductive cycle of male brown anoles (*Anolis sagrei*). *Physiol Zool* 71:139–146
- Verner J (1964) Evolution of polygyny in the long-billed marsh wren. *Evolution* 18:252–261
- Wiley RH, Poston J (1996) Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* 50:1371–1381
- Wingfield JC, Farner DS (1975) The determination of five steroids in avian plasma by radioimmunoassay and competitive protein-binding. *Steroids* 26:311–327
- Wirklund C, Fagerström T (1977) Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia* 31:153–158
- Workman SW, McLeod KW (1990) Vegetation of the Savannah River Site: major communities types. Savannah River Site Natural Environmental Research Park Progr, Dept Energy Publ SRO-NERP-19:1–137