INTERSEXUAL COMMUNICATION, MALE MATE PREFERENCE, AND REPRODUCTIVE ENERGETICS OF THE POLYGYNOUS LIZARD, *ANOLIS CAROLINENSIS*

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ABSTRACT

Particularly lacking in the current body of sexual selection literature are studies based on reptile species and intrasexually selected mating systems. Because the life history traits and ecology of reptiles are dramatically different from other animal taxa, current models of sexual selection are insufficient for predicting how sexual selection should influence the behavior and mating systems of lizards. Similarly, intersexually selected mating systems (i.e., based on female choice) are inappropriate predictive models for examining species with intrasexually selected mating systems (i.e., based on consexual contests). I investigated three aspects of *Anolis carolinensis* behavior and mating system (communication signals, male mate preference, and reproductive energetics) to contribute to a theoretical model for sexual selection based on a lizard with an intrasexually selected, polygynous mating system.

In my first study, I quantified the structure and use of signals exchanged by both sexes, compared signal structure and use during heterosexual interactions to that of other social contexts (e.g., male-alone, male-male, female-female), then related signal structure and use to the species mating system. During heterosexual interactions, both sexes performed three kinds of stereotypic headbob displays with equal precision that were essentially identical to those previously documented for other social contexts. Thus, there is no courtship-specific headbob display for *A. carolinensis*. However, male and female signal use was extremely dimorphic. For the purpose of indicating sexual identity, the sexually dimorphic patterns of signal use were excessively redundant, yet equivocal. Although the male pattern of signal use reliably conveys sexual identity, the female pattern of signal use conveys ambiguous sexual identity. Based on circumstantial evidence from other studies, I propose the hypothesis that the female pattern of signal use may permit female-sized, nonterritorial males to mimic female signals. Small males may be selected to use female mimicry to gain access to the territories of larger males and mating opportunities with resident females, while females may be indirectly selected to use a signaling pattern that provides them with an alternative mating option. From field and laboratory data on *A. carolinensis* signal behavior during other social contexts and the species' female-defense mating system, I evaluate proposed functions for heterosexual signaling from a perspective of intrasexual selection.

In my second study, I tested the prediction that males should include a preference for mating with novel females (PNF) as part of their mating strategy. This prediction was supported by both laboratory and field manipulations. Compared to their encounters with resident females, males during laboratory encounters with novel females significantly increased their display rate, volley frequency, volley length, and significantly decreased the distance and number of movements traveled away from the female. My laboratory data also suggest that males discriminated novel females from resident females independently of female behavioral or chemical cues. Similarly, compared to their interactions with resident females, free-ranging males responded to introduced novel females by significantly increasing the proportion of time spent in female-directed activities and the proportion of displays directed toward novel females, and significantly decreasing the proportion of time spent in territorial activities and the proportion of displays used in territorial activities. Data from both experiments indicate that males appear to distinguish among individual females, and use this ability to increase reproductive success by identifying and preferentially pursuing novel females over previously inseminated resident females. I suggest that males are able to cognitively identify individual resident females, and use this ability to control mating decisions within their territories.

In my third study, I examined the energy expenditure of males and females during breeding and postbreeding seasons. I used laboratory respirometry to determine resting metabolic rates, and the doubly-labeled water technique to determine field metabolic rates in free-ranging lizards. Resting metabolic rates were significantly influenced by body mass and season, but not sex. Field metabolic rates were significantly influenced by body mass, but not sex or season. I attributed the ~40% seasonal increase in resting metabolic rates to a seasonal increase in feeding rates and the effect of specific dynamic action. Resting and field metabolic rates were used to calculate energy budgets for each sex during breeding and postbreeding seasons, and to calculate the energy expended by each sex for reproduction. Despite having 40% smaller body mass, females expended 46% more energy for reproduction than males, and a similar amount of total maintenance energy as males. The total maintenance energy of males was similar during both seasons, however that of females decreased 44% from breeding to postbreeding season. I found both seasonal and sexual differences in the amount of energy lizards allocated to resting and activity. *Anolis carolinensis* had field metabolic rates that were similar to tropical and temperate species of lizards, and higher than lizards from arid/semiarid environments. *Anolis carolinensis* also expended more energy on eggs, and more total energy during the breeding season, than lizards from arid/semiarid habitats.

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Introduction

Overview

Behavioral ecologists strive to understand the ultimate reasons for why animals behave in the ways that they do. For the most part, evolutionary theories or adaptive explanations for animal behavior fall into two main categories: natural selection and sexual selection. The evolutionary mechanisms of natural and sexual selection developed by Darwin well over a century ago (1859, 1871) continue to provide biologists with powerful tools for examining how and why particular traits have evolved in species. For my thesis, sexual selection was the theoretical framework that best suited the interpretation of behavior patterns in the green anole, *Anolis carolinensis*. However, despite a large and ever growing body of literature on sexual selection, most studies have examined insect and avian species, and to a lesser extent, fish and amphibians (Andersson, 1994). Only a comparatively small number of sexual selection studies have examined reptiles. Because the life history traits and ecology of insects, birds, fish amphibians, and reptiles are dramatically different from each other, models based on non-reptile taxa are inappropriate or insufficient for predicting how sexual selection should influence the behavior and mating systems of lizards. In addition, the vast majority of studies have focused on intersexually selected mating systems featuring female mate choice, while studies on male mate choice and intrasexually selected systems (e.g., male contests or endurance rivalry) are relatively rare (Andersson, 1994). In this respect, my studies on *A. carolinensis* will contribute to developing a theoretical model for sexual selection based on a lizard with an intrasexually selected, polygynous mating system.

I investigated three aspects of *A. carolinensis* behavior and mating system. In Chapter 2, I describe the structure and use of communication signals by both sexes during heterosexual encounters, and related signal structure and use to the species mating system. In Chapter 3, I tested the hypothesis that intrasexual selection on *A. carolinensis* males has selected for a male-choice mating strategy in which males recognize and exhibit a preference for novel females (PNF) to increase their mating success. I conducted laboratory tests for the PNF response, then validated the lab results with field trials on free-ranging males. In Chapter 4, I examined the energetics of the *A. carolinensis* mating system, and tested hypotheses about the amount of energy each sex expends for reproduction, activity and maintenance. I also examined the energy expended by both sexes during the postbreeding season to compare how energy allocation to activity and maintenance changes as lizards shift to postreproductive activities.

1.1 Sexual selection

Sexual selection is an evolutionary process that occurs in sexually reproducing animals as a consequence of variation in individual traits, competition among individuals for mates, and nonrandom differences in individual mating success (Darwin, 1871). The theory of sexual selection was originally devised by Darwin to account for the evolution of conspicuous or exaggerated male traits that were unlikely to result from natural selection. Darwin observed that males often compete for mates, by fighting other males for access to females (intrasexual selection) or by persuading females to mate with them (intersexual selection). As the object of male competition, females tend to be the sex that mates with the winner, or chooses among potential mates. Sexual selection has thus resulted in the evolution of traits and/or behaviors that provide males with a mating advantage. Elaborate courtship behaviors, vivid colors, and other ornaments may enhance male attractiveness to females, and influence female mate choice. Structures that act as weapons, armor, or for intimidation of opponents may promote the success of males in contests over mates. Since elaborate and conspicuous structures and behaviors may attract the attention of predators, natural selection may contribute to females having less conspicuous traits and behaviors than males. More rarely, when males are the ones that choose to mate with females based on phenotypic traits, or when sex roles are reversed and females compete for access to males, sexual selection may result in females evolving conspicuous secondary sex characteristics (e.g., Berglund et al., 1986; Amundsen, 2000; Amundsen and Forsgren, 2001; Berglund and Rosenqvist, 2001)

Sexual selection occurs due to variance in reproductive success (Darwin, 1871). As an outcome of inter-male competition for mates, individual males vary in their reproductive success. In contrast, nearly all females find a mate and reproduce. Thus, male reproductive success is typically less assured and more variable than that of females, and the influence of sexual selection is relatively stronger on males than on females (Bateman, 1948). In polygynous mating systems, where the most competitive males mate with several females and the least competitive males do not mate at all, variance in male reproductive success and sexual selection on males is at an extreme. As a consequence, the relative variance in male and female reproductive success, and relative influence of sexual selection on males and females, is also at an extreme in polygynous mating systems. The dramatic difference in the intensity of sexual selection on polygynous males and females often results in sexually dimorphic traits and behaviors. Because males and females in monogamous mating systems are less divergent in the relative influence of sexual selection, monogamous species are much less likely to exhibit prominent sexual dimorphisms than polygynous species.

It was Bateman (1948) who first suggested that relative variance in male and female reproductive success, and the differing intensity of sexual selection on the sexes, was driven in part by the energetic costs of reproduction. Bateman observed that in most sexually reproducing species the initial energetic investment in offspring is typically much less for males (i.e., sperm) than for females (i.e., ova), and this disparity increases when gestation, egg production, or other means of parental care are provided solely by the female. Since females usually bear the bulk of the energetic burden in producing offspring, female reproductive success is limited by reproductive biology and resource availability, whereas male reproductive success is typically limited by the number of mates obtained. In species where males have low initial energetic investment in offspring, males may have substantial energy resources to compete for multiple mates, thus contributing to high variance in male reproductive success, intense sexual selection on males, and a polygynous mating strategy (Trivers, 1972; Emlen and Oring,1977). For species in which both sexes must provide parental care to achieve reproductive success (e.g., some birds with altricial offspring), males may only have enough energy resources to support one mate, resulting in a monogamous mating system (although social monogamy does not preclude males from sneaking copulations with additional females). More rarely, in species where sex roles are reversed and males provide the bulk of parental care (e.g., Oring and Lank, 1986, Berglund and Rosenqvist, 1993), females may be the sex that competes for and/or monopolizes multiple males, resulting in a polyandrous mating system. The environmental potential for one sex to monopolize multiple mates may also influence the evolution of mating systems. If mates or resources critical to reproduction are not spatially distributed so that they are economically defendable, then the environmental potential for polygamy is low (Emlen and Oring, 1977). Thus, life history traits and environmental constraints influence the various ways in which energy is channeled into reproduction, and these interacting factors drive the evolution of behavior patterns and mating systems.

Because of the intense sexual selection on males, and the large disparity of sexual selection on males and females, polygynous species provide excellent models for examining the influence of sexual selection on the evolution of traits, behaviors, and mating strategies. Polygynous species are more likely than monogamous species to exhibit traits and behaviors that have evolved due to extreme sexual selection, and to exhibit sexually dimorphic traits. In addition, because polygynous males and females typically have very different physiological and behavioral strategies for reproduction, polygynous species are also good models for examining the energy allocated to reproduction as a prime factor influencing the evolution of mating systems.

1.2 *Anolis carolinensis* as a model species

The green anole, *Anolis carolinensis,* is an excellent species model for examining the influence of sexual selection. First, the species is convenient. Endemic to and widespread over the southeastern U.S., *A. carolinensis* is easily obtained for laboratory studies, and conveniently located for field studies. Second, the species has been well studied. Many aspects of the species' life history and behavior are well documented, including detailed field studies describing the species' territorial and polygynous mating strategy (e.g., Greenberg and Noble, 1944; Fox, 1963; Licht, 1971; Ruby, 1984; Michaud, 1990, Jenssen et al., 1995; Nunez et al., 1997; Jenssen and Nunez, 1998; Jenssen et al., 2001). Third, the species exhibits sexually selected traits. The polygynous mating system of *A. carolinensis* (described below) is associated with intense sexual selection on males and sexually divergent mating strategies, and provides an excellent opportunity to examine the amount of energy allocated to these different reproductive strategies by each of the sexes.

A female-defense polygynous mating strategy is facilitated by *A. carolinensis* life history and ecology. With precocial neonates, both sexes are emancipated from post-hatch parental care (Gordon, 1956). Investing minimal energy directly in offspring allows males to direct their time and energy to maximizing their mating success, by engaging in inter-male competition and territorial defense. The distribution of females in relatively clumped, small (8 m^3), and stable home-ranges allows the most competitive males to defend large territories (69 m^3) that overlap an average of three resident females (Jenssen et al., 1995; Nunez et al., 1997). Since females produce single-egg clutches at about 1-week intervals for a four-month breeding season (Licht, 1971; Andrews, 1985a; Michaud, 1990), males attempt to defend their territories for as much of the breeding season as possible to maximize their reproductive success.

Consistent with expectations for a polygynous mating system, field observations indicate that intrasexual selection on *A. carolinensis* males is intense. In populations with a 1:1 sex ratio (Ruby, 1984; Jenssen et al., 1995), only a third of adult males succeed in defending a territory. With two-thirds of adult males having access to few or no females, territorial take-over, intrusion, and extra-pair matings are a constant threat to territorial males. Because females ovulate weekly and store sperm up to seven months (Fox, 1963; Andrews, 1985; Michaud, 1990), even one copulation with a male intruder could fertilize several of a female's eggs and severely reduce a territorial male's reproductive success. Lengthy (average 26 min) and repeated copulations between a resident male and each resident female (about several of a female's eggs and severely reduce a territorial male's reproductive success. Lengthy (average 26 min) and repeated copulations between a resident male and each resident female (about twice/week) may be a response to sperm competition and the possibility that females may have mated with other males (Jenssen and Nunez, 1998). To advertise their presence and monitor their territory for intruders, resident males traveled an average of 26 m/h and performed an average of 100 headbob displays/h (Jenssen et al., 1995). Because male reproductive success is contingent upon maintaining territorial defense for as much of the breeding season as possible, the mating strategy of males constitutes an endurance rivalry (Andersson, 1994). This long duration of male territorial activity is associated with loss in male body mass and an assumed 75% attrition rate in resident males by the end of the breeding season (Ruby, 1984).

In contrast to males, field observations indicate that intrasexual selection on female *A. carolinensis* is relatively weak. As an insectivorous, habitat generalist with no specialized nesting requirements (Nunez et al., 1997), resources to support female reproduction are readily available (Nunez et al., 1997). Within their small home ranges (8 m^3), females display infrequently (14 displays/h), rarely interact (about once/day), and are largely sedentary (move about 4 m/h), suggesting that inter-female competition for space or resources is minimal (Nunez et al., 1997).

Consistent with the differing intensity of intrasexual selection on males and females, and with selection for inter-male aggression, *A. carolinensis* exhibit sexual dimorphisms in morphology and behavior. In comparison to females, territorial males are 30-40% larger in body mass (Chapter 4), have a dewlap that is two-thirds larger, have eight-fold greater territory volume (69 m^3 vs. 8 m^3), move six-fold greater distances (27 m/h vs. 4 m/h), display seven-fold more frequently (100 displays/h vs. 14 displays/h), and spent a 30-fold greater proportion of the day in consexual dispute (9.2% vs. 0.03%) (Jenssen et al., 1995; Jenssen and Nunez, 1998; Nunez et al., 1997).

Within the female-defense polygeny of *A. carolinensis*, the opportunity to increase reproductive success through assortative mating (mate choice) is limited for both sexes, and thus the influence of intersexual selection on both sexes is weak. Males and females disperse into habitat simultaneously and females establish home-ranges in the early spring before breeding begins. Males then compete for volumes of habitat that encompass multiple female home-ranges just as females become reproductive (Jenssen et al., 2001). Since females are distributed in home ranges prior to the time that males establish territories, females mate by default with the male that gains control of the territory in which they reside (neutral-mate

1.3 Male mating strategies

There are typically three ways that males can maximize reproductive success: 1) males may monopolize and mate with as many females as possible by excluding them from other males, either through inter-male contests or territoriality; 2) males may persuade as many females as possible to mate with them, by attracting female attention and by influencing female choice; and, 3) males may participate in some form of mate choice. The type of mate choice strategy most frequently studied in males is quality-based discrimination, in which individuals increase reproductive success by choosing a mate that would produce greater numbers of offspring or superior offspring (reviewed in Andersson, 1994). Quality-based male mate choice has been documented for species in which female size, age, or condition is associated with fecundity (Gwynne, 1981; Verrell, 1989; Olsson, 1993), in species with female-biased operational sex ratios (Lawrence, 1986; McLain and Boromisa, 1987; Colwell and Oring, 1988; Kvarnemo and Ahnesjo, 1996), and species in which males provide the bulk of parental care (Gwynne 1981; Berglund & Rosenqvist 1993).

Male mate choice may also be based on factors other than female quality. Males should only expend time and energy to court and mate with a particular female if it would benefit their reproductive success. For example, male ground squirrels avoid copulating with a previously mated female if she is beyond the time when his sperm would have a good chance at fertilization success (Schwagmeyer and Parker, 1990). Similarly, male *A. carolinensis* lizards rejected 69% of mating opportunities with receptive resident females (Jenssen et al., 1995; Jenssen and Nunez, 1998). It is possible that male *A. carolinensis* reject mating with a resident female because they recently copulated with her, and since females store sperm (up to 7 months; Fox, 1963) and only ovulate a single-egg clutch about once a week, more than one copulation per week with the same female may not increase a male's reproductive success. Since copulations are time consuming (average 26 min in duration; Nunez and Jenssen, 1997), avoiding unnecessary copulations would maximize the time a male could spend defending his territory from other males and courting or mating with other females.

Another type of mate choice strategy is the preference for novel female response (PNF; e.g., the "Coolidge effect", Dewsbury, 1981). The PNF response would promote male reproductive success in the following way. If a male could determine whether a female represents a new mating opportunity, then he could optimize the time and energy expended on courtship and copulation by minimizing courtship toward previously inseminated females, and maximizing courtship efforts toward novel females. Given that males are able to discriminate among females, a PNF response would be expected for nearly any type of mating system, and especially for polygynous systems in which males are emancipated from parental care. Exceptions might be species for which mating with novel females results in reproductive penalties for males (e.g., monogamous species with biparental care requirements; Dewsbury, 1981). Despite the logical presumption that most males should exhibit a PNF response, the phenomenon has not been widely tested among taxa and mating systems (e.g., mammals, review by Dewsbury 1981; a salamander, Donovan and Verrell 1991; and four species of lizards: *Holbrookia propinqua*, Cooper, 1985; *Anolis sagrei*, Tokarz, 1992; *Eumeces laticeps*, Cooper, 1996; *Eublepharis macularius*, Steele and Cooper, 1997).

Prerequisite for the PNF response is the ability of a male to identify females previously inseminated from novel females that represent new mating opportunities, and to differentially respond to familiar and novel females in a way that benefits his fitness. At a basic level, the PNF response may be mediated by a stimulus-response type of mechanism involving a simple categorical discrimination between two classes of females (e.g., resident vs. novel females). This basic, categorical PNF response would require only that females exhibit some class-specific feature or behavior that would cue male discrimination and generate an appropriate male response. A PNF response may also be mediated by individual recognition of females, which requires that males have a cognitively-based ability to remember and identify individuals. Individual recognition may be considered a cognitive ability, in that subjects acquire, process, store, and use information from the environment to match contingent events with appropriate behaviour (Johnson, 1993; Dukas, 1998; Shettleworth, 1999). Mediated by individual recognition, the PNF response would require: 1) a temporal and spatial association between a male and one or more familiar females; 2) the male's ability to learn and memorize the particular features of individual females; 3), the male's ability to recall his mating history with a female (e.g., previous copulations); 4) the male's ability to recall the features of resident females and compare them to those of an encountered female; and, 5) when a male identifies a female as a resident or as a novel female, the male's ability to respond in a way that benefits his fitness (e.g., vigorously pursue a copulation with novel females to increase mating success).

Although only a few studies have examined whether lizards exhibit a PNF response, several studies provide evidence that lizards have the cognitive ability to recognize individual conspecifics (non-relatives). The ability to discriminate among individual conspecifics implies that many lizards may also have the cognitive ability to discriminate familiar resident females from novel females. Thus, below I have reviewed the studies that document both neighbor discrimination and mate discrimination in lizards.

Neighbor discrimination

The five studies described below suggest that male lizards can recognize their consexual neighbors. Also known as the “dear enemy” phenomenon (Fisher, 1954), neighbor recognition is based on the premise that territorial neighbors represent less of a threat than male intruders (Temeles, 1994). The dear enemy response occurs when territorial males exhibit less aggression toward males that are neighbors than toward males that are not neighbors, presumably to minimize the effort and risk associated with aggressive encounters.

Glinski and Krekorian (1985) examined neighbor discrimination in *Dipsosaurus dorsalis.* In one experiment, pairs of recently captured adult males were placed on either side of a divider in an outdoor arena (2.4 m X 1.2 m X .6 m high) outside the lizards' natural territories. After allowing 5 min for males to acclimate to the arena, the divider was removed and observations were made for up to 20 min. Two variables were measured; latency time to mutual challenge display (e.g., both lizards perform aggressive signals) and the distance between the lizards at their original capture location. The 46 trials indicated a significant negative correlation in the distance between the males’ natural territories and the time it took for males to perform aggressive displays. A negative aspect of this experiment was that some lizards were used from 1-6 times (an average of 1.6 times), and no indications were given as to whether lizards were subjected to successive tests, if lizards were given time for recuperation, or if precautions were taken to minimize handling effects. In a second experiment, each of 18 males were randomly paired with a neighbor and a non-neighbor using the same arena and procedure described above. Males performed aggressive challenge displays to non-neighbors significantly sooner than they did to neighbors (e.g., 9.7 vs. 18.3 min). Although this study supported neighbor discrimination in *D. dorsalis*, at least one male in a pair failed to respond aggressively to either neighbors or non-neighbors in 17 of 46 trials in the first experiment and six of 18 trials in the second experiment. The weak results of this study may have been due to the fact that lizards only had five minutes to familiarize themselves with the artificial ‘territory’ they were supposed to be defending. Use of natural territories, or acclimation periods of several days, may have provided better results.

Qualls and Jaeger (1991) reported neighbor discrimination in male *Anolis carolinensis*. An experimental cage (90 x 30 x 30 cm) was separated by nylon mesh into three equal compartments (30 cm^3), with two of the compartments also separated by a solid, opaque divider. A lizard was placed into each compartment and allowed at least 72 h for acclimation. After acclimation, the lizard in the center compartment was considered a 'resident' lizard, the lizard visible to the resident through the mesh was a 'neighbor', and the lizard not visible to the resident was a 'stranger'. Before each of the 20 trials, a second opaque divider was placed between the resident and neighbor compartments, and then the resident lizard was presented with the neighbor or the stranger by lifting the appropriate opaque divider. The amount of time a resident spent performing aggressive displays (headbob displays, dewlap extensions, gular inflation, and lateral presentation) was recorded for 10 min, then the opaque divider was replaced. After 1 - 2 h, the reciprocal lizard was presented in the same manner. The order in which a neighbor or stranger was presented was randomized among trials. Although resident males spent significantly more time performing aggressive behaviors towards strangers than towards neighbors (e.g., 57.8 vs. 1.2 s, respectively), nine male residents did not respond to either neighbors or strangers, and two males exhibited more aggressive behaviour toward their neighbor. Several factors may have contributed to the weak results of this study, including: only one variable was examined; experimental compartments were extremely small and did not contain reproductive females; there were no precautions taken to minimize observer effect (Sugerman,1990); and the duration of the observation periods was only10 minutes. In addition, male *A. carolinensis* exhibit consexual aggression only during the 4-month breeding season (Jenssen et al., 1995); if even a few of the trials were conducted outside of the breeding season (dates when the trials occurred were not provided), the males may not have been territorial.

The field study conducted by Fox and Baird (1992) provided more convincing evidence for neighbor discrimination in *Crotaphytus collaris* than the Qualls and Jaeger (1991) lab study on *A. carolinensis*. This study used 31 free-ranging males in their natural territories. Resident males were presented randomly with a tethered male that was either a neighbor (individuals that were natural, established neighbors) or a stranger (captured > 5 km away) at the edge of their territory. Observations were recorded for 10 min, and the reciprocal half of the trial was conducted at least 1 day later. Resident males responded to tethered neighbors with significantly fewer aggressive acts and significantly less intense aggression than toward tethered strangers, and a longer latency time to aggression (the latter was not statistically significant).

Individual recognition has also been reported for male sand lizards, *Lacerta agilis* (Olsson, 1994). In each of eight laboratory staged encounters using 16 captive-born males, two males were placed on either side of a divided enclosure (0.5 X 1.2 m). After the males acclimated to the cage for 30 min, the divider between the males was removed so the males could interact. Five hours later, a second encounter was staged between the same pair of males using the same procedure as in the first encounter. Encounters ended when one lizard, the loser, exhibited a submissive chin-lowering behavior. Contests during the second staged encounters were significantly shorter (mean duration of seven seconds) than during the first encounters (mean duration of 178 s). The author suggested that males recognized a familiar opponent in the second encounter, and that a shorter contest resulted from inferior males (the loser in an encounter) adjusting their aggressive behavior to avoid an escalated encounter with a male that won the previous contest. Since the large home-ranges of male sand lizards overlap widely, males are likely to meet and interact repeatedly while searching for mates. If secondary encounters between males have predictable outcomes, recognition of familiar male rivals may function to reduce the intensity and duration of subsequent aggressive interactions. The study could have been improved by using a larger sample size, by using a control comparison (e.g., males paired with a non-familiar male for the second encounter), and by using additional and longer intervals between successive encounters (i.e., free-ranging males in the field may encounter familiar individuals at intervals of days or weeks rather than hours). In addition, the study used captive-bred males that were artificially hibernated for six weeks prior to the study, then isolated from other males and females. The author did not state whether males were actually in breeding condition. In general, the laboratory-staged protocol was far from ideal in that males were not defending actual resources or mates, and they may have had little motivation to continue aggressive interactions during second encounters.

Neighbor discrimination has also been reported for the territorial lizard, *Platysaurus broadleyi* (Whiting, 1999). In 12 manipulated field trials using free-ranging lizards in their natural territories, bread crumbs were thrown to decrease the separation distance and stimulate agonistic encounters between residents and their neighbors, and between residents and non-neighbors. Resident males allowed neighboring males to approach significantly closer than non-neighboring males before initiating aggression, were significantly more aggressive toward non-neighbors, and chased non-neighbors significantly further than neighbors. In 10 natural field trials (no bread-crumb manipulations), natural encounters were observed between male residents and their neighbors, and the same residents and non-neighbors. Although the natural encounters between resident males and neighbors were significantly longer than with non-neighbors, they were significantly less aggressive than those between resident males and non-neighbors. In both manipulated and natural encounters, residents won more contests with non-neighbors than with neighbors, interactions with neighbors were more likely to end in a draw, and residents ignored neighbors more frequently than they did non-neighbors.

Mate discrimination

Six studies have been published on mate discrimination in lizards, all of which examined whether males can discriminate familiar females from novel females. Two studies on monogamous species of lizards reported that males preferred to associate with and follow their familiar mate. In 19 of 26 trials, male snow skinks, *Niveoscincus microlepidotus,* ignored the scent path of a vitellogenic female they had not copulated with to follow the scent path of the vitellogenic female they had copulated with through a maze (Olsson and Shine, 1998). The ability of male snow skinks to identify and follow their mates was presumed to facilitate mate guarding during the extended 6 - 11 month period between copulation and fertilization. In sleepy lizards, *Tiliqua rugosa*, a male and female form a monogamous pair for a period of about 6 weeks during the breeding season, during which time they alternate periods of staying together for several days with several days of separation (Bull et al., 1998). About 77 - 80% of the pairs over three years were found to re-pair with the same mate for 2 - 3 subsequent breeding seasons. Long-term associations between males and females, and the ability of separated pairs to relocate each other after several days or months, requires that individuals can discriminate their mates from other individuals. Females have even been shown to relocate their partners after natural or experimental separation (Bull et al., 1993). Although mate guarding may be one advantage of monogamy in *T. rugosa*, the authors cannot explain the strong tendency for pairs to rejoin for subsequent breeding seasons.

The PNF response has been reported for four species of polygynous lizards. The first study (Cooper, 1985) presented free-ranging male *Holbrookia propinqua* with tethered females. Males were presented alternately with one of their resident females, and a novel female. Females were tethered 0.6 m away from resident males. The social behaviors exhibited by each male were recorded until the male stopped courting, or attempted to force copulation, then the relative intensity of courtship exhibited by males during each interaction was ranked (e.g., no courtship < stationary shudder < shuddering approach < persistent courtship and/or attempt to grab female’s neck < persistent attempt to force copulation, multiple attempts to grab female’s neck). Unfortunately, the methods of the study did not specify whether precautions were taken to minimize observer effect on the lizards (e.g., blinds), how long the trials lasted, or how much time was given between resident and novel female presentation, and it did not examine the effect that tethering females had on male or female behavior. Although two males fled after females were presented, the courtship of 7 of the remaining 12 males in the study was significantly more intense (based on the ranking of behaviors described above) toward novel females than toward resident females. Five males courted resident and novel females with equal intensity, and none of the males courted resident females more intensely than novel females. Males were also more likely to attempt forced copulations with novel females than with resident females. Cooper noted that there were no obvious behavioral differences between resident and novel females that might have cued or influenced male courtship, inferring that the male PNF response exhibited by *Holbrookia propinqua* could be mediated by individual discrimination among females.

Tokarz (1992) reported mate discrimination and the PNF response in *Anolis sagrei*. In the first of two lab experiments, 32 male *Anolis sagrei* were each housed separately with a female for 16 days (familiar females). Then, on the 17th day, the familiar female was removed. After 30 min, both the familiar female and a novel female (a female that was housed with a different male for 16 days) were simultaneously introduced into the male's cage. The number of copulations that occurred between the male and each female was recorded for the next 12 h. The second experiment on 12 males was conducted in exactly the same way as the first experiment, except that the familiar and novel females in the second trial were size matched. Males copulated about three times more frequently with novel females then with familiar females, and males courted novel females even when the females were unreceptive to mating. Male preferences for novel females could not be explained by female traits (e.g., body size, reproductive condition) or by any apparent differences in female behaviours (e.g., displays, receptiveness to mating), including class-specific behaviours (e.g., resident vs. novel females) that might have indicated a more basic stimulus-response mediated PNF. Thus, Tokarz's study suggests that the PNF response in *A. sagrei* is also based on individual discrimination.

The PNF response reported for the leopard gecko *Eublepharis macularius* (Steele and Cooper, 1997) and the skink *Eumeces laticeps* (Cooper, 1996) appears to be mediated by chemical cues. In both studies, males were presented with chemical stimuli obtained from novel and familiar females (moist cotton swabs with cloacal secretions, Cooper, 1996; moist cotton balls rubbed over skin surfaces, Steele and Cooper, 1997). In comparison to cloacal stimuli from familiar, cagemate females, male *E. macularis* responded to cloacal stimuli from novel females with a significantly higher rate of tongue-flicks, a higher probability of performing a tail vibration courtship behaviour, and a higher probability of remaining with the chemical source during a trial. A similar result was reported for *E. laticeps* in that males tongueflicked toward cloacal stimuli of novel females about twice as frequently as toward cloacal stimuli of familiar females. In presenting males with chemical stimuli rather than live females, both studies reduced or eliminated the potentially confounding effects of female body size or behaviour on male preferences, and both studies support the idea that these species are using chemical cues to distinguish among familiar and novel females. Geckos may also use skin-based chemical cues in sex discrimination (Mason and Gutzke, 1990; Steele and Cooper, 1997), and skinks have been shown to use chemical cues to discriminate conspecifics from heterospecifics (Cooper and Vitt, 1986; Cooper and Garstka, 1987) and to follow female scent trails to locate and guard females from other males (Vitt and Cooper, 1985; Cooper and Vitt, 1987). Although the chemically-mediated PNF response in *E. macularis* and *E. laticeps* could be an example of cognitively-based individual discrimination, males may simply be discriminating among two classes of females via a stimulus-response type of mechanism (e.g., male self-recognition of semen and/or other male-based substances deposited on a familiar female during prior copulation or social interactions).

The studies described above suggest that several lizard species can and do discriminate among non-related individuals, and that in some species, individual discrimination appears to be based on the cognitive ability to learn and remember the features of individual females, to recognize the novel features of non-familiar individuals, and to respond to the identity of conspecifics with behaviors that will benefit the fitness of the responder. The studies above also suggest that the PNF response is associated with polygynous rather than monogamous mating systems. The PNF response would benefit the reproductive success of males only when there are few or no reproductive penalties for mating with multiple females. For instance, the reproductive success of some monogamous males may be reduced when males pursue matings with more than one female, perhaps because females must be guarded to protect paternity, or because reproductive females are widely distributed and difficult to find. However, males in a socially monogamous mating system may still exhibit the PNF response if they seek out extra-pair matings to increase their reproductive success, or if they exhibit serial monogamy.

I predicted that the lizard, *A. carolinensis*, was a likely candidate for the PNF response. The polygynous mating system, life history traits, and social organization predispose this species to the PNF response for several reasons. First, the intense level of intrasexual selection among polygynous males predicts that males should utilize any available mating strategy that would increase their reproductive success. Second, precocial and independent offspring emancipates both sexes from parental care, so males have no parental obligations to restrict or penalize them from mating with multiple females. Third, the clumped distribution of females in small, stable, overlapping home ranges presents territorial males with a potential array of familiar and novel females. Fourth, the four-month breeding season provides a territorial male ample opportunity to learn the features of individual resident females, a condition for contrasting the uniqueness of novel females, and a greater chance that males may encounter reproductive novel females than a short breeding season. Fifth, since females can store sperm for a period that spans the entire breeding season and 13 - 16 ovulatory events (Fox, 1963; Andrews, 1985a; Michaud, 1990), a male that succeeds in copulating even once with a novel female could fertilize as many as 16 of her eggs. Sixth, territorial males passed up 69% of mating opportunities with receptive, neck-bending resident females, indicating that males may have the cognitive ability to recognize individual females, and that they are under selection to optimize the amount of time and energy expended for courtship and copulatory behavior (Jenssen and Nunez, 1998).

The goals of my study on the PNF response were to: 1) determine whether male *A. carolinensis* can discriminate among resident and novel females, and whether they exhibit the PNF response within a laboratory setting; 2) determine the type of discrimination (e.g., categorical or individual) involved in the PNF response; 3) identify the potential factors or cues used to mediate the PNF response; and, 4) determine whether the PNF response is used by free-ranging lizards, and to describe the expression of the PNF within a natural setting.

1.4 Anoline communication signals

The signals and patterns of signal use that evolve in a species result from complex interactions among species-specific constraints and selective pressures, including (but not limited to): life history traits, sensory bias (e.g., structures and/or physiology involved in signal production and perception; Endler, 1992; Alberts, 1992; Endler and Basalo, 1998), environment (e.g., habitat light and structure constrain signal perception; Alberts, 1992; Endler and Thery, 1996; Fleishman et al., 1997) and natural selection (e.g., signal detection by parasitoids, predators, and prey; Endler, 1983; Endler, 1987; Orrell and Jenssen, 1994). Because communication signals mediate conspecific encounters, and they may relay information about the identity and/or quality of individuals, signals may have a strong influence on the outcome of consexual and heterosexual encounters. As such, the structure and use of communication signals are closely associated with social organization and reproductive success, and thus are strongly influenced by sexual selection (Endler, 1983; Wagner and Reiser, 2000).

The conspicuous visual communication signals of anoline lizards provide excellent subjects for examining selective influences on signal evolution. Anoles perform stereotypic and species-specific headbob displays (Carpenter, 1965) that are coordinated with the extension of a colorful and extendible display organ, the dewlap (Font and Rome, 1990). Signals are thus a combination of movement and color. The perception of headbob displays is facilitated by a highly motion and color sensitive visual system (Makaretz and Levine, 1980; Fite and Lister, 1981; Fleishman, 1992). The distance at which headbob signals can be perceived by conspecifics is influenced by the amplitude of display head and/or body movements and by dewlap extension (Fleishman, 1988). The extended dewlap provides color and/or brightness contrast against background habitat and light conditions, and creates an effective leading edge that enhances the detection of headbob movements (Fleishman et al., 1997; Persons et al., 1999; Macedonia, 2001). When not in use for signaling, the dewlap is retracted, perhaps to keep it out of the way during locomotion, or to minimize detection by predators.

It has been suggested that anoles use headbob displays for functions such as territorial advertisement (e.g. Greenberg and Noble, 1944), intimidation of opponents (e.g. Greenberg and Noble, 1944; Cooper, 1977; DeCourcy and Jenssen, 1994), to attract mates and coordinate mating (e.g. Evans, 1938; Greenberg and Noble, 1944; Jenssen, 1970; Crews, 1975; Cooper, 1979), and even to deter predators (e.g., Leal, 1999). Although anoline headbob displays have been implicated in female mate choice, experiments conducted to date have failed to find consistent evidence to support female preferences for particular male display traits (Greenberg and Noble, 1944; Crews, 1975; Sigmund, 1983; Andrews, 1985b; MacDonald and Echternacht, 1991; review by Tokarz, 1995). It has also been proposed that headbob displays serve as cues for individual recognition in lizards (e.g., Cooper, 1985; Glinski and Krekorian, 1985; Quails and Jaeger, 1991; Fox and Baird, 1992; Tokarz ,1992; Olsson, 1994; Bull et al., 1998; Olsson and Shine, 1998; Whiting, 1999), although none of these studies have determined exactly what cues are used to assist in recognition.

Species-specific displays and dewlap coloration have long been thought to serve as species isolating mechanisms (e.g. Rand and Williams, 1970; Jenssen, 1971; Williams and Rand, 1977; Losos, 1985; Macedonia and Stamps, 1994). Initially, the idea that species-specific headbob displays serve as reproductive isolating mechanisms was quite strongly advanced for *Anolis* species because of the added nuance of species-typical dewlap colours among parapatric and sympatric congeners (e.g. Ruibal, 1967; Rand and Williams, 1970; Webster and Burns, 1973; Williams and Rand, 1977). However, experimental evidence for display signals as a criteria of species identification is quite limited. Jenssen and Gladson

(1984) inferred a species recognition function for headbob patterns in the sibling species *A. websteri* and *A. caudalis* based on pattern characteristics that were more divergent in sympatric than in allopatric populations. Subsequently, an experiment by Jenssen (1996) found that *A. websteri* females did not discriminate between mating with conspecific males or *A. caudalis* males. Only one study examined female preferences for males with conspecific displays; female *A. nebulosus* demonstrated a preference for filmed versions of normal male displays rather than altered male displays (Jenssen, 1970). Sigmund (1983) reported that female *A. carolinensis* preferred a normal red dewlap color, or a dewlap color with high contrast to the background. In contrast, other studies found that *A. carolinensis* females did not particularly prefer males with conspecific dewlap color (Crews, 1975; MacDonald and Echternacht, 1991), and that female mating preferences may be influenced by the ability of males to extend the dewlap rather than dewlap color (Greenberg and Noble, 1944; Crews, 1975; Tokarz, 2002).

Some authors have suggested that male anoles may also use display signals to discriminate conspecifics from sympatric cogeners during inter-male encounters. Male *A. grahami* and *A. marcanoi* discriminated video play-backs of displaying conspecifics from heterospecifics (Macedonia and Stamps, 1994; Macedonia et al., 1994), however the signals used for discrimination (e.g., dewlap color, size, or shape, body color or morphology, headbob cadence pattern) were not determined. In examining the responses of male *A. marcanoi* and *A. cybotes* (sympatric, sibling species that differ morphologically only in dewlap color) during conspecific and heterospecific encounters, Losos (1985) found that dewlap color appeared to influence species discrimination more than display cadence. *Anolis marcanoi* males exhibited strong aggression toward normal conspecifics, intermediate aggression toward heterospecifics with red painted dewlaps (to mimic conspecifics) and incorrect headbob patterns, and weak aggression toward conspecifics with white painted dewlaps (to mimic *A. cybotes*) and correct headbob patterns.

To advance our understanding of how and why signals evolve, and to elucidate potential signal functions, the structure and use of signals must be examined in relation to the particular selective venues that signals are used in. In this respect, there are three conspecific social contexts for signal exchange: non-directed signaling, where there is no targeted recipient (advertisement context, e.g., male-alone and female-alone); directed signaling toward a consexual (an aggressive context, e.g., male-male and female-female); and directed signaling toward a heterosexual (courtship context, e.g., male-female). Previous studies on anoline communication signals have almost exclusively focused on males during consexual contexts (e.g., Jenssen, 1971; Jenssen and Hover, 1976; Jenssen, 1977; Jenssen, 1979; Jenssen, 1983; Jenssen and Gladson, 1984; Bels, 1986; Font and Kramer, 1989; DeCourcy and Jenssen, 1994; Jenssen et al., 2000). Female display signals have been examined for only three species (e.g., *A. aneus*: Stamps, 1973; *A. bahorucoensis*: Orrell and Jenssen, 1998; *A. carolinensis*: Jenssen et al., 2000), and only two studies examined display signals during the courtship context (Scott, 1984; Orrell and Jenssen, 1998). The male bias in anoline signaling studies may be due to a perception that male displays are functionally more important than female displays; males usually have larger dewlaps then females (Schwartz and Henderson, 1991), and male headbob displays are often associated with territorial advertisement and defense, and mate attraction (Carpenter, 1982). However, both sexes of anoles use stereotyped display signals, and since selective influences on males and females are usually very different, it seems logical that the signals of both sexes should be included in studies examining the evolution of signal design and use.

The green anole, *Anolis carolinensis*, is an excellent subject for the study of sexually selected effects on communication behavior because the species female-defense polygyny is well documented (e.g., Ruby 1984; Jenssen and Nunez, 1998; Jenssen et al., 2001), and provides the opportunity to examine signal expression within an intrasexually selected mating system (Emlen and Oring 1977). The polygynous mating system of *A. carolinensis*, and the sexually divergent mating strategies and behavioral profiles of *A. carolinensis* (see Introduction), strongly suggest that this species should exhibit sexually dimorphic signal behavior. Previous studies on consexual signaling in male and female *A. carolinensis* (DeCourcy and Jenssen, 1994; Jenssen et al., 2000) revealed that both sexes performed the same three stereotyped cadence patterns (type A, B and C displays), and that displays of both sexes were equally stereotyped. However, male and female signal use differed greatly, and these differences reflect the relative influence that intrasexual selection has on the signaling behavior of each sex. Males during consexual encounters performed displays at extremely high rates (168 displays/h), used all three display types, dewlap extension, and display volleys in a shifting pattern as the distance between two opponents decreased, and exhibited a ritualized pattern of consexual combat (e.g., circling, jaw-sparring and jaw-locking; Jenssen, 1979; DeCourcy and Jenssen, 1994). Signal use during inter-male encounters reflects the importance of display signals to male reproductive success within a female-defense polygyny mating system; male fitness is largely dependent on the outcome of male contests and territorial defense (Jenssen et al., 1995; Nunez et al., 1997). Multiple display types used in frequent and ritualized signal exchange between male opponents may function in opponent assessment and bluff, thus decreasing the risk of physical fighting and injury (Jenssen, 1977, 1978; Ord et al., 2001).

In contrast, signal use during inter-female encounters reflects relatively weak intrasexual selection on females. Females during consexual encounters displayed at modest rates (17 displays/h), primarily used a single display type (78% type C displays), and did not exhibit shifting signal use or ritualized aggression. Unlike males, females have little to gain through consexual contests; small (8 m^3), overlapping (20%) female home ranges and infrequent competitive interactions between neighboring females (about once/day) suggest that competition among females for space and resources is minimal (Nunez et al., 1997; Jenssen and Nunez, 1998).

My study examines male and female *A. carolinensis* signal structure and use during the heterosexual context, thereby completing the analysis of the species display signals during all social contexts. Despite numerous studies that anecdotally described courtship behavior in *A. carolinensis* (e.g., Greenberg and Noble, 1944; Crews, 1975 ; Ruby, 1984; Andrews, 1985b), the form and use of signals exchanged during heterosexual interactions have never been quantitatively described or analyzed. Female *A. carolinensis* displays were described as rhythmic headnods that lack a distinct pattern (Crews, 1975; Greenberg, 1977) even though female displays were not actually quantified. Sigmund (1978) reported that female displays were similar to those of males, but performed with a much lower amplitude. Yet none of these studies presented statistical analyses, visual representations of male or female displays (e.g., a display-action-pattern graph), or descriptions of the stereotyped display patterns (display types) that are characteristic of the genus (Carpenter, 1986).

Based on *A. carolinensis* polygynous mating system (Jenssen and Nunez, 1998; Jenssen et al., 2001), and male and female behavioral profiles (Jenssen et al., 1995; Nunez and Jenssen, 1997; see Introduction), I had three general expectations for signal behavior during the heterosexual context. First, I expected no courtship-unique signals for either sex. Selection for a courtship-unique signal would most likely occur if one or both sexes were highly mobile and dependent on long-range attraction signals for locating potential mates, especially if one or both sexes had a limited reproductive season. However, male and female *A. carolinensis* occur in close proximity (males compete for territories containing 2 - 4 resident females and mate primarily with resident females) and have a long, four-month breeding season (Jenssen and Nunez, 1998; Jenssen et al., 2001). Second, I expected that displays used during heterosexual interactions would have similar structural features as displays described for consexual contexts (e.g., DeCourcy and Jenssen, 1994; Jenssen et al., 2000). Since consexual contests are important to male fitness, the species' signal design and display repertoire should strongly reflect the influence of intrasexual selection on males. In contrast, there is little evidence to suggest that mating decisions of either sex are based on display use during heterosexual interactions (Jenssen and Nunez, 1998; Orrell and Jenssen, 2002). Thus, intrasexually selected signal traits may be conserved in signals used during heterosexual interactions. Third, because both sexes share the same repertoire of aggressive signals (e.g., Jenssen et al., 2000), I expected that males and females will also have a common repertoire for heterosexual signaling. However, signals may be used in a sexually dimorphic manner, with potential functions for heterosexual signal use (e.g., coordinate courtship and mating, identifying species, sex, and individual identity) accomplished by the choice and frequency of signals used.

My study accomplished four goals: 1) I described and analyzed signal behaviors used by both sexes during heterosexual encounters; 2) I compared the structure and use of signal behaviors during heterosexual encounters to that of other social contexts (i.e., non-directed and consexual); 3) I evaluated possible signal functions; and, 4) I identified possible correlates between the species signal behavior and mating system.

1.5 Energy expended for reproduction

The relative intensity of sexual selection on each sex, and the type of mating system that evolves in a species, is related in part to the relative amount of energy that each sex allocates for reproduction (Bateman, 1948; Orians, 1969; Trivers, 1972; Arnold and Duvall, 1994). Typically, females invest more energy directly in offspring than males (e.g., eggs, vitellogenesis, gestation, lactation vs. sperm). When males contribute paternal care to offspring, both sexes may allocate a similar amount of energy in reproduction. If care-giving males do not have the energy or time to pursue multiple mates, a monogamous mating system usually results. Males emancipated from parental care typically have the time and/or energy resources to defend or pursue multiple mates, contributing to a polygynous mating system. Although polygynous males may invest little energy in individual offspring, they may still allocate energy to reproduction as structures and/or behaviors that increase their mating success. For example, males may allocate energy to attain large body size or to develop specialized structures (e.g., large canines, elaborate plumage; Halliday 1987) that provide a competitive advantage in consexual aggressive interactions fought over females and/or territories, or that influence female mate choice (Andersson, 1994). Males often expend energy for reproductive activity to advertise and defend their territory, and/or the females residing within, from male competitors (Jenssen et al., 1995; Marler and Moore, 1991; Marler et al., 1995), or to attract and/or court potential mates. For example, males of many species expend energy to perform song (e.g., birds, frogs and insects; reviewed by Halliday, 1987; Ryan, 1988; Borgia,1993), and courtship rituals or displays (Vehrencamp et al., 1989; Kotiaho et al, 1998).

Because most animals expend at least some energy for reproduction in the form of activity, it can be difficult to determine the total amount of energy expended for reproduction. One way to estimate the amount of energy expended for reproductive activity is to use energy budgets to partition the total energy assimilated by an organism into energy allocated to maintenance, activity, and storage (Congdon et al., 1982). The partitioning of an energy budget requires several types of data: 1) rates of temperature-specific resting metabolism (determined in captive, inactive subjects using laboratory respirometry); 2) temperature profiles of field active subjects (e.g., the amount of time animals exhibit particular body temperatures); 3) rates of daily field energy expended by free-ranging subjects [rates of total energy expenditure, determined using the doubly labeled water (DLW) technique; Nagy, 1975]; and, 4) estimates of the amount of energy allocated to egg production by females. Temperature profiles are used in combination with rates of maintenance metabolism to estimate the total amount of resting energy expended (i.e., while sleeping or inactive, plus the inactive portion of energy expended while active). Then, the amount of daily energy expended on activity can be calculated as the difference between daily field energy and daily resting energy. The energy expended for activity during the breeding season can then be included in estimating the amount of energy expended by each sex for reproduction (e.g., as energy that males allocate for reproductive activity, and energy that females allocate to activity and egg production).

Previous research on laboratory measured rates of metabolism in lizards has revealed many factors that influence maintenance metabolism. In addition to body mass and body temperature (Andrews and Pough, 1985), maintenance metabolism is influenced by: activity level (e.g., sleeping, alert and inactive, or alert and active; Bennett and Gleeson, 1979; Morgan, 1988), digestion (specific dynamic action; Waldschmidt, 1987; Niewiarowski and Waldschmidt, 1992; Secor and Phillips, 1997), season (Tsuji, 1988; Rismiller and Heldmaier, 1991; Zari, 1996), and time of day (Rismiller and Heldmaier, 1991; Niewiarowski and Waldschmidt, 1992; Beapre et al., 1993). Acclimation of subjects to captive conditions may also confound laboratory measurements (Beyer and Spotila, 1994). A number of previous studies measured *A. carolinensis*' metabolic rates in the laboratory (e.g., Dessauer, 1953; Maher and Levedahl, 1959; Ragland et al., 1981; Gatten, 1985; Gatten et al., 1988; Wilson and Gatten, 1989; Jenssen et al., 1996). However, since the aforementioned studies determined rates in fasted lizards obtained commercially and/or held in the laboratory for several weeks or months, these data are not suitable for partitioning an energy budget. Rather, respirometry on lizards freshly captured from the field

(< 24 h) provides metabolic rates of lizards digesting food (from prey consumed prior to capture), avoids acclimation of subjects to lab conditions, and most closely approximates the resting energy of free-ranging lizards.

There have been six studies that examined energy expenditure in reproductive lizards: Congdon, (1977), Bennett and Nagy (1977), Nagy (1983), Anderson and Karasov (1988), van Marken Lichtenbelt et al. (1993), and Karasov and Anderson (1998). Although each of these studies utilized the doubly labeled water method for determining daily field energy, methods for determining maintenance metabolism varied greatly (e.g., some studies used fasted rather than fed lizards, or lizards were held in the laboratory for extended periods), as did methods for calculating the energy expended for reproduction. In reviewing these studies below, I compared male and female rates of daily field and maintenance energy, total energy expended during the breeding season, and where possible, the energy expended for reproduction.

One of the earliest studies to quantify the energy expended for reproduction in lizards is that of Bennett and Nagy (1977), who examined the energy expended by *Scelopurus occidentalis* during breeding and postbreeding seasons. Neither sex nor season influenced rates of daily field energy (averaged 136 J/g/day and 122 J/g/day for breeding and postbreeding seasons, respectively) or maintenance metabolism. Although the study did not calculate energy expended for reproduction, an energy budget partitioned daily field energy into resting and activity energy. I estimated the energy expended for reproduction as activity energy expended by males (105 kJ/season), and activity energy plus egg production for females (151 kJ/season). Both sexes had similar body mass (11.9 g), but females expended about 25% more total energy than males during the 120 day breeding season (including egg production, 232 vs. 186 kJ, respectively). However, there are several problems with the study's estimate of resting energy. Fasted lizards appear to have been used to determine maintenance metabolic rates, which would have underestimated resting energy and overestimated activity energy by 25-50% (Niewiarowski and Waldschmidt, 1992). Maintenance metabolic rates were measured in a dark chamber at night, and rates used to calculate the energy budget were not adjusted for alert animals during the day (Andrews and Pough, 1985). Although maintenance metabolism was measured as O_2 consumption and CO_2 production, only CO_2 production was used to calculate resting energy. Since reptiles may excrete CO_2 in fecal urates, CO_2 production may not be as accurate as O_2 consumption for measuring metabolism (Grigg, 1978; Schmidt-Knielsen, 1990). And finally, this study used lab-acclimated lizards. Due to factors that may vary seasonally (e.g., photoperiod, the amount and type of food consumed, activity, fat stores utilized or deposited), lab metabolic rates measured on lab-acclimated lizards may not be the same as those of free-ranging lizards.

Another early study examined the energy expended for reproduction by *Sceloporus jarrovi* (Congdon, 1977). During the breeding season, males had significantly higher rates of daily field energy than females (120 J/g/day vs. 82 J/g/day, respectively, Turkey Creek population). To calculate an energy budget, resting metabolic rates were estimated from a formula derived from standard metabolic rates of several lizard species (published by Bennett and Dawson, 1976), and were adjusted for the influence of specific dynamic action, but were not adjusted for alert lizards during the day. Congdon estimated the energy expended for reproduction by females as energy allocated to egg production only. The energy expended for reproduction by males was estimated as the difference between male and female activity energy (female activity energy was considered a ‘maintenance level expenditure’, and the amount of activity energy males expended above that was considered to be for male reproductive activity). For a 61 day breeding season, Congdon estimated that a 13 g male and 13 g female (including egg production) would expend about the same amount of total energy (98 kJ/season vs. 101 kJ/season, respectively) and about the same amount of energy for reproduction (33 kJ/season vs. 36 kJ/season, respectively). However, males are typically larger than females (the extent of sexual size dimorphism varies with population), and an average sized 13.0 g female and 15.7 g male (mean masses of second year breeding adults used in study) would differ by about 12% in total energy expenditure (115 kJ/season for females vs. 101 kJ/season for males) and about 11% in energy expended for reproduction (40 kJ/season for females vs. 36 kJ/season for males). This study revealed significant age-related variance in the energy expended for reproduction; both sexes increased the energy allocated to reproduction with age. By their third year of breeding, males and females allocated 900% and 300% (respectively) more energy to reproduction than during their first breeding season.

Nagy (1983) determined the daily field energy expended by *Uta stansburiana* at monthly intervals for an entire year. In early spring (February-April), when males were establishing territories, male rates of daily field energy (averaged 149 J/g/day) were significantly higher than those of 2-yr old females (averaged 113 J/g/day). In later months (May-July), when females were laying eggs and males were no longer territorial, female rates of daily field energy (averaged 209 J/g/day) were significantly higher than those of males (averaged 161 J/g/day). The energy expended for reproduction was estimated by the authors as the difference in daily field energy expended by reproductive and nonreproductive lizards, plus egg production for females. For two breeding seasons totaling 117 days in duration, a 3.7 g male *U. stansburiana* would expend about 28% more total energy than a 2.4 g female (64 kJ vs. 50 kJ, respectively), but 110% less energy than a 2.4 g female for reproduction (21.5 kJ vs. 45.1 kJ). This study did not examine resting metabolic rates, however, and the estimated amount of energy expended for reproduction may be inaccurate if resting metabolic rates actually differed seasonally.

Anderson and Karasov (1988) examined the energy expended by *Cnemidophorus tigris* during breeding and postbreeding seasons. Males, who were larger than females (18.8 g vs. 15.7 g, respectively), had significantly greater rates of daily field energy than females during the breeding season (299 J/g/day vs. 255 J/g/day, for males and females, respectively). Males expended 23% more total energy than females (including egg production) over the 52-day breeding season (507 J vs. 413 J, for males and females, respectively). Although both sexes have a wide-searching foraging strategy, males had larger home ranges and higher activity rates than breeding females. Both sexes expended more daily field energy and had higher activity rates during the breeding season than during the postbreeding season (by 18 and 42%, for males and females, respectively). This study did not calculate an energy budget (i.e., partition daily field energy into resting and activity energy), nor did it estimate the energy expended for reproduction. Resting metabolic rates were determined (in fed lizards), and were similar for both sexes. However, the methods did not specify during which season measurements were made, or whether lizards were captured from the field or held in the laboratory prior to measurements.

Karasov and Anderson (1998) also examined the energy expended by *Callisaurus draconoides* during breeding and postbreeding seasons. Rates of daily field energy were measured for both sexes at two different geographic locations, during two different breeding seasons (April-May 1980, August-September, 1978), and during the postbreeding season (June 1979). Rates of daily field energy were not significantly influenced by sex or study site, but those during the August-September breeding season (143 J/g/day and 163 J/g/day for males and females, respectively) were significantly higher than during the April-May breeding season and the postbreeding season (by 15-18% for males, and 20-32% for females). Males were larger than females (10.5 g vs. 8.0 g, respectively), and males expended 23% more total energy then females during the 52-day April-May breeding season (507 J vs. 413 J for males and females, respectively). This study did not calculate an energy budget, or estimate the energy expended for reproduction. Although resting metabolic rates were determined in fed lizards, and during breeding and postbreeding seasons, the data still suffer from some serious drawbacks. Measurements during the breeding season were made so late that some lizards may not have been reproductive, many lizards were held in the lab for several weeks prior to measurements, and some measurements were repeated on the same individuals at different temperatures. Resting metabolic rates were also determined on lizards from two different geographic locations, during different years, and using different measurement methods. With so much variation in how resting metabolic rates were measured, it is not surprising that there were no detectable differences in them due to sex, season, or site.

The energy expended by *Iguana iguana* during breeding and postbreeding seasons was examined by van Marken Lichtenbelt et al. (1993). Rates of daily energy expenditure were similar for both sexes and both seasons (78 J/g/day and 72 J/g/day for breeding males and females, respectively, 71 J/g/day and 69 J/g/day for postbreeding males and females, respectively). A 1004 g female would expend about 146% more total energy than a 713 g male during a 60-day breeding season (based on the average size of males and females in the study; 3,320 kJ for males vs. 8,178 kJ for females including egg production). This study did not estimate energy expended for reproduction, but based on their data I calculated that a 713 g male would expend about 1,892 kJ for breeding season activity, and a 1004 g female would expend about 6,317 kJ for breeding season activity plus egg production. Problems with this study include small sample sizes (n = 2 females and 3 males during the breeding season), and an incomplete presentation of the methods and results. For example, the clutch size used to calculate energy expended for egg production was not stated, the energy budget did not specify the time period it was calculated for, and no mention was made as to whether the males in this study were territorial. Resting metabolic rates were measured for both fasted and fed lizards, but the methods did not state how long lizards were held in the laboratory prior to measurements, or the season in which measurements were made.

Because body mass has a strong influence on energy expenditure, sexual dimorphism in body mass may contribute to a sexual disparity in energy expenditure. To summarize trends for the studies described above, females expended more energy for reproduction than males in three species (by 44% in *S. occidentalis*, 110% in *U. stansburiana*, and 234% in *I. iguana*), and males expended more energy for reproduction than females only in *S. jarrovi*, although the difference was only 11% (two studies did not determine energy expended for reproduction). In three of the species examined, females expended more total energy during the breeding season than males (by 10% in *C. draconoides*, 25% in *S. occidentalis*, and 146% in *I. iguana*), while in the other three species males expended more total energy than females (by 14% in *S. jarrovi*, 23% in *C. tigris*, and 28% *in U. stansburiana*). Male-larger sexual size dimorphism (by 20-50%) may have contributed to male *S. jarrovi*, *C. tigris*, and *U. stansburiana* having greater total energy expenditure during the breeding season than conspecific females. However, for *I. iguana*, the large sexual disparity in the energy expended for reproduction (233%) and total energy expended during the breeding season (146%) is only partially attributable to females having 30% larger body mass than males. Similarly, *S. occidentalis* males and females were similar in body mass, and females still expended 44% more energy for reproduction than males, and 25% more total energy during the breeding season. Despite being 50% smaller than conspecific males, female *U. stansburiana* expended 110% more energy than males in reproduction. Thus, in some species, females may indeed expend more energy for reproduction than males.

The amount of energy expended by males and females for reproduction is also influenced by reproductive strategies, life history traits, and/or ecology. With the exception of *C. tigris* and *I. iguana*, the lizard species in the above studies are polygynous, the males have a territorial mating strategy, they live in arid/semi-arid habitats, have an insectivorous diet, and use an ambush-style foraging strategy. *Cnemidophorus tigris* is also a polygynous, desert, insectivore, but both sexes employ an extremely active wide-searching strategy for finding food and mates that results in a very high rate of daily field energy expenditure compared to other desert species (Anderson and Karasov, 1988). Adjusting for interspecific differences in body size (e.g., kJ/body mass$^{0.8}$; Nagy, 1999), *C. tigris* expends more total energy for the entire breeding season than all of the other species compared (the average for males and females is 47.0 kJ/g$^{0.8}$ vs. 13.4 kJ/g$^{0.8}$ for *S. jarrovi*, 23.7 kJ/g$^{0.8}$ for *U. stansburiana*, 24.9 kJ/g$^{0.8}$ for *I. iguana*, 30.1 kJ/g$^{0.8}$ for *S. occidentalis*, and 30.4 kJ/g$^{0.8}$ for *C. draconoides*). *Iguana iguana* is a tropical, wide-foraging, herbivore that is much less likely to be water or food limited than desert species, and would therefore be expected to have greater energy resources available for reproduction. Of the four species compared, *I. iguana* females expended the greatest amount of energy in reproduction (adjusting for interspecific differences in body size; 25.1 kJ/g$^{0.8}$ vs. 4.6 kJ/g$^{0.8}$ for *S. jarrovi*, 20.8 kJ/g$^{0.8}$ for *S. occidentalis*, and 22.4 kJ/g$^{0.8}$ for *U. stansburiana*).

Other aspects of life history also influence the energy expended for reproduction, and complicate studies that attempt to quantify this energy. For instance, all of the lizards compared above are to some extent ‘capital’ breeders that use at least some energy that is collected and stored prior to breeding for reproduction (Jonsson, 1997). Only two of the above studies accounted for the use of stored energy for reproduction in their calculations (e.g., Congdon, 1977; Nagy, 1983). It may be difficult in some cases to determine how much of the energy expended for reproduction was accrued prior to breeding, and what the energetic cost of obtaining and storing those resources might be. In contrast, ‘income’ breeders rely mostly on energy obtained during the breeding season for reproduction (Jonsson, 1997), and quantifying this amount of energy is much more straightforward than for capital breeders. Further complicating estimates of energy expended for reproduction is whether a species typically breeds for one season only or for multiple seasons, and in the latter case whether the amount of energy expended for reproduction varies with age (e.g., Congdon, 1977; Nagy, 1983). In addition, during some years but not others, environmental fluctuations (e.g., droughts) may influence the food and/or water availability and in turn, the energy expended for reproduction. Clearly more studies are needed to determine how various factors impact the energy lizards expend for reproduction to better understand the evolutionary relationships between energy expenditure, mating systems, and reproductive traits and behaviors.

The lizard *Anolis carolinensis* provides several advantages for examining the energy allocated to reproduction by males and females. Unlike many lizards, *A. carolinensis* are income breeders rather than capital breeders (i.e., energy allocated to reproduction is derived from daily energy intake, not from energy stores accumulated prior to the breeding season; Dessauer, 1955; Wade, 1981), greatly simplifying the task of quantifying the energy expended for reproduction. The species is a good subject for the DLW technique because both sexes have low vagility during the breeding season (males are territorial and females have stable home-ranges), which allows lizards to be captured for isotope injection and blood sampling, released back into the field, and then several days later recaptured from the same area for collecting a second set of blood samples. In a temperate habitat with regular precipitation (at least in most of the species range), *A. carolinensis* is unlikely to be energy limited by unpredictable or low food and/or water availability as species in arid habitats typically are.

Anolis carolinensis is also a good species for examining energy allocated to reproduction because the species polygynous mating system, field behavioral profiles, and life history are well documented, and suggest several testable hypotheses. Since offspring are precocial and independent, neither sex expends energy for post-hatch parental care. Territorial males expend the vast majority of energy for reproduction as activity. Males advertise and defend their territory by performing an average of 100 headbob displays/h, and patrolling and traveling 26 m/h (Jenssen et al., 1995). Territorial males spend about spend 10% of their day in aggressive interactions with rival males, and 8% of their day displaying towards and copulating with females (Jenssen et al., 1995; Nunez and Jenssen, 1997). Only a third of males are able to defend territories, which typically overlap the home-ranges of 2-6 resident females (69 m^3; Nunez and Jenssen, 1997). The remaining males without a territory or direct access to females are believed to constantly challenge or intrude on territorial males. Since females lay about one egg per week throughout the four-month breeding season (Andrews, 1985a; Michaud, 1990), males maintain territorial defense for as much of the breeding season as possible. That territorial males lose body mass and have an apparent 75% attrition rate by the end of the breeding season (Ruby, 1984) suggests that males expend a great deal of energy on territorial activity, and that they expend more energy than they consume. For females, the majority of energy expended for reproduction is to produce eggs, and the energy expended for reproductive activity appears minimal. In contrast to territorial males, females during the breeding season are relatively sedentary, performing < 14 displays/h and traveling < 40 m/h in small (8 m^3) home-ranges (Nunez et al., 1997). After the breeding season, both sexes have a relatively inactive behavioral profile similar to that of females during the breeding season (Jenssen et al., 1995).

Based on the mating strategies and behavioral profiles of both sexes, I formed three general predictions. First, as a result of the presumed high energy demands of male territorial activity (e.g., territorial defense, consexual interactions, courtship, and copulation) and female egg production, I predicted that the amount of energy expended for reproduction by males is similar to that expended by females. Second, due to the dramatic difference in activity between highly active territorial males and relatively sedentary females, I predicted that the amount of energy expended for activity is greater for males than for females during the breeding season. Third, because of the cessation of reproduction (e.g., territorial activity, egg production) and sedentary levels of postbreeding activity in both sexes, I predicted that the transition from breeding to postbreeding season should be associated with a decrease in total energy expenditure and activity energy expenditure for both sexes.

My goals for this study were to: 1) collect the field and laboratory data required to calculate daily energy budgets for both sexes during breeding and postbreeding seasons; 2) compare rates of resting metabolism and daily field energy to determine the influence that sex and season have on metabolism (independent of intersexual differences in body size); 3) use energy budgets to test the predictions above; 4) relate energy expenditure to the particular mating strategy and life history traits of *A. carolinensis*; and 5) compare the energy expended for reproduction by *A. carolinensis* to that of other lizard species.

Summary

The life history traits and polygynous mating system of *Anolis carolinensis* provide an excellent opportunity for examining the evolution of behavior patterns and mating systems in relation to intrasexual selection. Each of my three studies addresses a different aspect of the *A. carolinensis* mating system that should be strongly influenced by sexual selection, but have rarely been examined by previous studies. Despite a plethora of descriptive studies on anoline headbob displays, only two previous studies (DeCourcy and Jenssen, 1994; Jenssen et al., 2000) have examined how the structure and use of these communication signals is influenced by sexual selection. Yet, in coordinating social interactions and facilitating male and female reproductive success, communication signals are an integral part of male and female mating strategies. My study will reveal how the signal structure and patterns of signal use relate to the influence of sexual selection in the species' polygynous mating system. Similarly, a number of studies have examined female mate choice in lizards and found little evidence to support the idea. In contrast, only a few studies have examined whether male lizards might play a more active role in mate choice, and what strategies males use for choosing mates. Intense intrasexual selection on males, and the particular characteristics of the *A. carolinensis* mating system, suggest that males should exhibit specific behavioral responses that increase male mating success, and thus male fitness. The ability to discriminate among individual females and identify new mating opportunities (i.e., novel females), and then to pursue new mating opportunities, is a behavioral strategy that could increase male mating success, and thus should be strongly selected for. Finally, the activities that males and females depend on to achieve reproductive success (e.g., male territoriality, female egg production) are directly limited by the amount of energy required to perform them. Much of sexual selection theory is based on economic models concerning the energy that each sex expends for reproduction (e.g., the concept that females initially invest more energy directly in offspring than males), yet very few studies have actually quantified the energy that each sex expends for reproduction. My study will determine the amount of energy that both sexes expend for reproduction, and examine how that relative investment relates to the behaviors used to accomplish reproductive success, and the species' polygynous mating system. Together, my three studies on the communication signals, male mate preference, and reproductive energetics of *A. carolinensis* will expand current models of sexual selection by using a reptile as a model species, and contribute toward a better understanding of the inter-relationships between life-history traits, behavior, energetics, and the evolution of particular mating systems.

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CHAPTER 2

Heterosexual signalling by the lizard *Anolis carolinensis*: effects of an intrasexually selected mating system

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Abstract

We quantified the structure and use of signals exchanged by males and females within the female-defense polygyny of the lizard, *Anolis carolinensis*. In this mating system, male fitness is favoured by large body size and intense territorial activity to guard resident females. During heterosexual interactions, both sexes performed three kinds of stereotypic headbob displays (types A, B, and C) with equal precision. These three display types were essentially identical in structure (i.e., cadence pattern of head movement) as the A, B, and C display types previously documented for both sexes during consexual contests, and for males when displaying alone (non-directed context). Therefore, there is no courtship-specific headbob display for *A. carolinensis*. Although interacting males and females displayed at a similar mean frequency (~20 displays / h), they signalled in the following sexually dimorphic manner: (1) males used predominately type C displays (89%), whereas females used predominantly the type A and B displays (48% and 50%, respectively); (2) males extended their dewlaps with almost every display (98%), whereas females extended their dewlaps with few displays (< 2%); (3) males sequenced 80% of their displays in volleys of two or more displays, whereas females performed only 12% of their displays in volleys; and (4) males concluded 22% of their displays with shudderbobs (i.e., display modifier composed of a series of shallow, quick, double bobs), whereas females never appended their displays with shudderbobs. From a broad base of *A. carolinensis* data (i.e., field and laboratory data on signal behaviour during other social contexts and the species' female-defence mating system), we interpret heterosexual signalling from a perspective of intrasexual selection to explain: (1) the absence of a courtship-unique display, (2) the physical structure of displays, (3) size of display repertoire, and (4) the likelihood of species and individual recognition. For indicating sexual identity, the antithetical use of display types and dewlap by the sexes was excessively redundant, and yet, equivocal. Because females avoid extending their sexually dimorphic dewlaps to males (seven fold smaller for an average sized female than an average sized male), sex identification of females remains problematic. Thus, we propose a female mimicry hypothesis for the pattern of heterosexual signalling. By signalling ambiguously, females permit female-sized males to mimic female signals, thereby providing an alternative mating option to females. Small males that used this deceptive strategy could gain access to the territories of larger males to practice kleptogamy with resident females.

Introduction

Animals signal one another to coordinate and influence the social activities that are critical to mating success. As such, sexual selection should affect most aspects of a communication system in ways that facilitate male and female reproductive success within a given mating system. Additionally, within given mating systems, sexual selection may vary between the sexes, resulting in some degree of sexual dimorphism in signalling structures, signal repertoires, and patterns of signal use (Andersson, 1994; Bradbury and Vehrencamp, 1998). This is particularly true of polygynous mating systems, where polygynous males have much greater variance in reproductive success than females, and consequently experience stronger sexual selection than females (Bateman, 1948). Thus, males of polygynous systems usually have enhanced signals for consexual competition (i.e., intrasexually selected effects) and/or for mate attraction (i.e., intersexually selected effects). Conversely, females rarely show the same degree of signal elaboration as polygynous, conspecific males (Bradbury and Vehrencamp, 1998) and may even lack signals analogous to those of males (e.g., Thornhill and Alcock, 1983; Searcy and Andersson, 1986; Searcy and Yawasaka, 1994). Because general theorems of sexual selection predict obvious sexually dimorphic effects on their communication systems, polygynous species are useful subjects for examining signal evolution. Furthermore, by examining species with well documented mating systems, predictive models for signal evolution can be more easily derived and tested by accumulating case studies that relate specific signal traits used by males and females to their known social activities.

The mating system.—The green anole lizard (*Anolis carolinensis*) is an excellent subject for the study of sexually selected effects on communication behaviour because its female-defence polygyny is well documented (e.g., Ruby, 1984; Jenssen and Nunez, 1998; Jenssen et al., 2001) and provides the opportunity to examine male and female signal expression within an intrasexually selected mating system (Emlen and Oring, 1977). DeCourcy and Jenssen (1994) and Jenssen et al. (2000) analyzed consexual signalling by male and female *A. carolinensis*, and found that the structure and use of headbob displays largely followed expectations for signals that are subject to intrasexual selection. However, lacking robust models, clear predictions as to how heterosexual signalling should evolve within the intrasexually selected mating system of *A. carolinensis* were elusive. To clarify the selective effects on heterosexual signals and to suggest relevant hypotheses to guide our study, an understanding of the spatial and social organization of the sexes was critical.

Characterization of the *A. carolinensis* mating system begins with the distribution of reproductive females in time and space, because the reproductive traits of females largely determine the reproductive response of males (e.g., Partridge and Endler, 1987; Davies, 1991; Sutherland, 1996). Temporally, females lay single-egg clutches at about weekly intervals (Andrews, 1985a; Michaud, 1990) throughout a 4-month breeding season (Jenssen et al., 1995). Spatially, females move from overwintering shelters into home ranges prior to the breeding season (Jenssen et al., 2001), then remain in relatively stable, small (~ 8 m^3), overlapping (~ 20%), and lightly defended (~ one aggressive encounter/day) home ranges during the breeding season (Nunez et al., 1997; Jenssen and Nunez, 1998). The small female home ranges and infrequent competitive interactions between neighboring females suggest that the resources needed for egg production are not critically limited (Jenssen and Nunez, 1998).

In response to clumped, sedentary, and iteroparous females, males attempt to monopolize multiple females by means of long-term territorial defence (Ruby, 1984; Jenssen et al., 1995). Inter-male contests for habitat containing females result in a 1:3 male-to-female polygyny ratio in populations with 1:1 adult sex ratios (Ruby, 1984; Jenssen et al., 1995). As a consequence of female-defence territoriality, the potential reproductive rate among territorial males is positively correlated with male body size, size of male territory, number of defended (i.e., resident) females, as well as the duration of the male on his territory (Ruby, 1984; Jenssen and Nunez, 1998). Selection for inter-male aggression in *A. carolinensis* may contribute to prominent sexual dimorphisms. In comparison to females, males are 30–40% larger in body mass (Jenssen et al., 1995; Orrell, 2002), have seven-fold greater dewlap area (1.52 cm^2 versus 0.22 cm^2; Jenssen et al., 2000), have eight-fold greater territory volume (69 m^3 versus. 8 m^3), move six-fold greater distances (27 m/h versus.4 m/h), display seven-fold more frequently (100 displays/h versus. 14 displays/h), and spent a 30-fold greater proportion of the day in consexual disputes (9.2% versus. 0.03%) (Jenssen et al., 1995; Nunez et al., 1997; Jenssen and Nunez, 1998).

Mate choice.—Within the female-defence polygyny of *A. carolinensis*, the mechanism of mate choice differs between the sexes. Females appear to employ indirect mate choice (i.e., passive choice, sensu Wiley and Poston, 1996). Females, by being sedentary (Nunez et al., 1997) and closely spaced (Jenssen and Nunez, 1998), attract local males. Ensuing inter-male contests produce a minority of males who can establish and maintain stable territories containing multiple females (Ruby, 1984). Territorial males then serve as the primary mates for their respective resident females (Jenssen and Nunez, 1998). Thus, the offspring of resident females receive paternal traits that were selected for by territorial contests (e.g., large body size, aggressiveness, fighting ability, and a robust physiology for stamina and good health). Since they do not actively select mates, *A. carolinensis* females fit the neutral-mate-choice model (sensu Lightbody and Weatherhead, 1988; Jenssen and Nunez, 1998).

Mate choice by males appears to emphasize quantity of mates, and not quality. Jenssen and Nunez (1998) found no evidence for assortative mate choice for selected variables (i.e., male body size and territory size were not correlated with female body size, home-range size, and potential reproductive rate). However, Jenssen and Nunez did find that male potential reproductive rate was correlated with number of defended females. A quantitative response to mating was further documented for males by their pronounced preference for novel females over resident females (Orrell and Jenssen, 2002).

Guiding hypotheses.—Given the details of the species' mating system (above), we pose three general hypotheses to guide our analysis of heterosexual signalling. First, we predict no courtship-unique signals in either sex. Selection for a courtship-unique signal would most likely occur where one or both sexes were mobile and dependent on an attraction signal by the opposite sex for localization of potential mates (e.g., female frogs moving to calling males, Howard, 1978; or male snakes moving to pheromone-emitting females, Ford, 1986). Selection for a mate attraction signal would be particularly pronounced if one or both sexes had a limited temporal window for reproduction. In contrast to the latter conditions, females of *A. carolinensis* establish their home ranges before breeding begins. Then local males become territorial, and for up to four months defend and mate primarily with females already resident within their patrol areas (Jenssen and Nunez, 1998; Jenssen et al., 2001). Thus, where long-term mates occur in close proximity to one another, a courtship attraction signal would seem superfluous.

Second, we predict that the structural features of displays used during the heterosexual context should be similar to the displays used for non-directed (i.e., territorial advertisement) and consexual contexts (e.g., DeCourcy and Jenssen, 1994; Jenssen et al., 2000). Given the reproductive importance of consexual contests in the mating system of *A. carolinensis*, especially for males, signal design and display repertoire should strongly reflect the influence of intrasexual selection. Conversely, because there is little evidence to suggest that mating decisions of either sex are based on display use during heterosexual interactions (Jenssen and Nunez, 1998; Orrell and Jenssen, 2002), intersexual selection on signals should be relatively weak. Thus, we expect that intrasexually selected signal traits may be conserved in signals used during heterosexual interactions.

Third, we expect that if males and females share a common display repertoire that is primarily influenced by intrasexual selection (e.g., Jenssen et al., 2000), then the sexes should use the signals in their shared repertoire in a sexually dimorphic manner. Thus, potential functions for heterosexual signal use (e.g., identifying species, sex, individuals, and interest in mating) may be accomplished by the choice and frequency of signals used.

To find support for our three predictions, we: 1) describe the structure and use of heterosexual display behaviour by *A. carolinensis*; 2) compare signal behaviour during heterosexual interactions with that during consexual and non-directed social contexts; and 3) draw inferences on possible signal function relative to the mating system of *A. carolinensis*. Ultimately, our analysis will initiate generalizations for the evolution of heterosexual signals within a seemingly male-controlled mating system.

Methods

Seventeen adult males [mean snout–vent length (SVL) 58.7 ±1.24 SE mm)] and 17 adult females (mean SVL 50.7 ±SE 1.76 mm) of *A. carolinensis* were collected during the breeding season from the Savannah River Site in Aiken, South Carolina, and brought to our laboratory at Virginia Tech. They were grouped into 17 male/female pairs, with each pair held separately in 0.6 H x 0.6 W x 0.7 L m wooden cages for 1–3 weeks prior to observations. For observations, each pair was moved to a 0.6 W x 0.6 x 1.2 L m wooden enclosure with a front wall of glass. The glass was slanted away from the cage at the top, and covered on the inner surface with a fine nylon screen to minimize the prospect that lizards might see and respond to their own reflections. All cages and the observation enclosure were furnished with tree trunks, branches, artificial foliage, and soil substrate, and illuminated by 1.3 m long, 40 W fluorescent bulbs and 150 W incandescent floodlights (200-300 lux; LI-COR model LI-185B photometer). The photoperiod was kept on a 12L:12D cycle to facilitate reproductive condition (Licht, 1971). Cage temperatures were about 24ºC at night, and 28–35ºC during the day, but could reach 42ºC directly under a floodlight. Vitamin-dusted crickets, waxworms, and sprayed water were provided daily.

We conducted 17 trials of heterosexual interactions using 17 separate pairs of lizards. For each trial, we moved a male/female pair to the observation enclosure, and allowed the lizards three days to acclimate. Then we videotaped spontaneous interactions for three hours from a darkened blind 1.5 m in front of the observation cage, through a 5 cm H X 140 cm L opening. We used two cameras (Panasonic Model WV-1550 and Vicon 16–160 mm zoom lenses) to provide enlarged images of each lizard. Output from the two cameras was simultaneously recorded to a video cassette recorder (Panasonic Model AG-1950) with a split screen generator (Vicon Model V270SP, P8). Elapsed time in 0.01 s intervals was also recorded to the videotape by a time-date generator (Odetics Model G-77).

The most complex and almost exclusive class of signals performed were headbobbing displays. The quantitative analysis of these displays required frame-by-frame analysis. We followed the methods of DeCourcy and Jenssen (1994) by plotting the head amplitude and dewlap extension over time. The resulting display-action-pattern graphs (DAP graphs, sensu Carpenter and Grubitz, 1961) were divided into naturally occurring units of bobs and interbob pauses. The cadence of bobs and pauses within a display was used to sort the displays into several reoccurring patterns that we refer to as ‘display types'. Following the convention of DeCourcy and Jenssen (1994), display types were labelled by a letter designation (e.g., A, B, C), and display units were numbered based on a perceived homology among display types (see DeCourcy and Jenssen, 1994). Analysis of each display type concentrated on the “core” units (i.e., the units always performed for a display type, sensu Jenssen, 1977). Display unit durations were measured to the nearest 0.033 s. We limited DAP graph analysis of male displays to five subjects (chosen at random from the 17 males) because male headbob displays have previously been analyzed (e.g., DeCourcy and Jenssen, 1994; Lovern et al., 1999; Jenssen et al., 2000). The remainder of male displays were classified into types by visual inspection of the videotape record.

Headbob displays were analyzed for stereotypy using descriptive statistics [mean ±standard error (SE) and coefficient of variation (CV = SD /mean * 100)]. As a convention, we considered behavioural units with a CV < 35% to be highly stereotyped (Barlow, 1977). Comparisons were made with non-parametric Kruskal-Wallis tests. Sequential Bonferroni adjusted P-values (SBON) were used for multiple comparisons within a group to reduce possible type I errors (Rice, 1989). For sex and context comparisons, a mean value for each subject was used as an individual observation to eliminate bias due to unequal numbers of sample sizes among subjects. Nested analysis of variance quantified sources of display variance (e.g., context, sex, subject, and error), and multivariate discriminant procedures were used to compare the displays of individual subjects. All statistics were computed with SAS version 6.12 (SAS Institute, Inc., 1989), and were two-tailed with an overall a = 0.05.

For each display performance, the following variables were recorded from videotapes: (1) signaller identification; (2) signaller sex; (3) display type; (4) whether the dewlap was extended (i.e., the coloured throat fan adapted for signalling, described by Bels, 1990; Font and Rome, 1990); (5) whether the display were performed singly or as part of a volley (i.e., two or more displays <2 s apart); (6) if the display were part of a volley, what was its position in the sequence of displays; and (7) whether the display was accompanied by non-headbob movements and postures (i.e., dynamic and static modifiers associated with the display behaviour, sensu Jenssen, 1979). In addition, because signal use may be correlated with the distance between signaller and recipient, we estimated the inter-subject separation distance for each display performance using a tape measure affixed to the bottom front of the observation cage. Displays were assigned to one of five classes of inter-subject separation distances: 1 (1–20 cm), 2 (21–40 cm), 3 (41–60 cm), 4 (61–80 cm), and 5 (>80 cm).

We compared display structure and use during heterosexual interactions with those from other social contexts. These data for *A. carolinensis* were available for the male nondirected context (i.e., male-alone; DeCourcy and Jenssen, 1994), male-male context (DeCourcy and Jenssen, 1994), and female-female context (Jenssen et al., 2000). The inter-study comparisons were facilitated by identical or comparable housing and observation conditions, recording equipment, recorded variables, and analysis protocol.

Results

Display types.—DAP graph analyses were made on 336 female displays and 126 male displays from heterosexual interactions. Three distinct display type patterns (i.e., A, B, and C) were observed (Fig. 2.1). Males and females performed each display type with near identical precision. The core portion of all three display types ended with unit 11, followed by 0–4 optional units (98% of displays included or ended with unit 13, and 22% of displays ended with unit 15). When comparing durations for homologous units, none of the 33 units from the three display types significantly differed between the sexes (Kruskal-Wallis, SBON, $P > 0.001$), nor did the total display duration for the cores of the three display types (Kruskal-Wallis, $P > 0.06$; Table 2.1)

The cadence patterns of the type A, B, and C displays performed during courtship were nearly identical to those previously described for consexual male and consexual female contexts (Jenssen et al., 2000). Of the 48 unit durations and six total display durations compared, only the durations of units 8 and 9 of female type A displays and the total duration of female type A displays were significantly different between heterosexual and consexual contexts (Kruskal-Wallis, SBON, $P = 0.017–0.002$; Figs.

2.2 and 2.3). However, in spite of very similar durations for homologous units, there was a significant trend for male and female displays performed during courtship to have shorter bob units (19 of 24 units; Chi-square test, $X^2 = 8.2$, $P < 0.004$, df = 1), longer pause units (22 of 24 units; $X^2 = 16.7$, $P < 0.001$, df = 1), and a longer total duration of units 1–10 (6 of 6 comparisons) than displays during consexual contexts (Figs. 2.2 and 2.3).

Display stereotypy.—The unit durations within type A, B, and C displays were highly stereotyped in both sexes. Within-subject unit CVs (calculated for each subject separately) ranged 0–71.7%. Of the 578 display units analyzed for individual lizards, only 13 units had CV values >35%. Average within-subject unit CV values were 14.9, 13.0, and 10.7% for female type A, B, and C displays, respectively, and 20.9, 13.8, and 17.5% for male type A, B, and C displays, respectively. Among-subject CV values, where intra-subject mean unit durations were used as single datum, ranged 3.6–52.9% (Tables 2.1 and 2.2), and only three of 54 unit CV values were >35%. Average among-subject CV values were 15.1, 15.6, and 15.1% for female type A, B, and C displays, respectively, and 25.4, 11.9, and 13.7% for male type A, B and C displays, respectively. Odd-numbered bob units tended to be more stereotypic than even-numbered pause units (Kruskal-Wallis tests, P = 0.0001–0.002 for display types of both sexes pooled , Table 2.2), and the frequency of this trend was greater than would be expected by chance (22 of 24 units, Chi-square test, $X^2 = 16.7$, $P <0.001$, df = 1).

Sources of display unit variance.—Combining our data with those available for males and females during consexual contexts (see Methods), we used a nested ANOVA procedure to partition display unit variance according to context, sex, among-subject, and within-subject components (F-tests were not computed due to unbalanced data). Context (e.g., heterosexual, consexual male, and consexual female) and sex contributed very little to unit variance of each display type; the mean unit variance attributed to context ranged 10.4–19.3%, and to sex ranged 6–15% (Fig. 2.4). Differences among and within individual subjects were the two largest sources of display unit variance. Within each display type, the average proportion of unit variance due to differences among subjects ranged 25–33%, and that due to differences within subjects was slightly greater, ranging 37–50% (Fig. 2.4). When display unit variance was examined by bobs and pauses, bob unit durations tended to vary less among subjects than within subjects (10 of 12 bob units) and, conversely, pause unit durations tend to vary more among subjects than within subjects (7 of 12 pause units; Fig. 2.4).

Individual differences.—Although displays were highly stereotyped, inter-subject differences in display cadence were sufficient that a multivariate discriminant analysis could frequently identify the displays of individual subjects. Using units 1–13 of male and female displays performed during the heterosexual context, nearest neighbor discriminant analysis correctly identified the subjects for 86.4% of type A displays, 83.1% of type B displays, and 79.2% of type C displays.

Display modifiers.—Besides the stereotyped headbob displays, the only other obvious signal performed was a display modifier (i.e., an optional movement or posture added to a headbob display, sensu Jenssen, 1977). This modifier, performed only by males, was appended to the end of a display, and fits the description of “shudderbob” (sensu Tinkle, 1967). Shudderbobs were a variable series of shallow double bobs (Fig. 2.5) that terminated 22% of male displays. Shudderbob amplitude was 30–50% that of the last bob in the display. From 15 DAP graphed sequences, shudderbobs: began after a brief pause (0.15 ±SE 0.01 s) following the last bob of a display (i.e., unit 11, 13, or 15); averaged 5.5 bobs in a sequence (±SE 0.38); and individual bobs had short and variable duration (0.1– 0.6 s / bob). Shudderbobs were not associated with any particular display type, being performed with 28% of type A, 26% of type B, and 23% of type C displays (Cochran-Mantel-Haenszel Statistic, F = 1.03, P >0.31). Shudderbobs accompanied 12% of single displays (i.e., not in a volley) and 25% of volleyed displays. When a display within a volley was accompanied by shudderbobs, the position of the modified display within the volley was random (Cochran-Mantel-Haenszel Statistic, F = 0.008, P >0.92). The only other display modifiers performed by males were two incidences each of raised crest and gular extension. Female displays were not accompanied by any modifiers.

Signal use.—Although both sexes performed about 20 displays per hour (19.2 ±3.40 displays / h for males, 21.7 ±3.12 displays / h for females; Table 2.3), and tended to perform displays at short (0–60 cm) rather than long (>80 cm) inter-subject separation distances (Cochran-Mantel-Haenszel Statistic, F = 8.79 for females, 5.01 for males, P <0.025; Fig. 2.6), four pronounced sexual dimorphisms in signal use were found. First, females performed mostly type A and B displays (A:B:C ratio of 24:25:1), while males performed mostly type C displays (A:B:C ratio of 1:1:16; Fig. 2.6, Table 2.3). Second, females mostly performed displays singly (88%) rather than in volleys (12%), whereas males performed most displays in volleys (80%; Fig. 2.7, Table 2.3). Third, dewlap extension rarely accompanied female displays (<2%), and almost always accompanied male displays (99%; Table 2.3). Fourth, females used no modifiers with their displays, while males terminated 22% of their displays with shudderbobs (Fig. 2.5, Table 2.3).

Possible correlates of signal frequency.—We examined whether the frequency of male signalling might reflect relative arousal level or body condition. Our assumptions were that display rate should correlate positively with motivation level, and good body condition (due to energy reserves) should facilitate greater levels of signalling. If the assumptions are correct, display rate should covary with other signalling variables, and/or body condition should covary with signalling behaviour. Under our laboratory conditions, however, we found neither to be the case. Male display rate did not significantly correlate with: the tendency to display in volleys, the use of shudderbobs, female display rate, female neck-bends (sign of sexual receptivity, Crews, 1973a), or with copulation (Fisher's exact test, P = 0.6–1.0). Similarly, neither male body mass nor body condition (body mass / SVL * 100) correlated with male display rate, proportion of displays in volleys, or proportion of displays with shudderbobs (Fisher's exact test, P = 1.0).

Heterosexual signal use compared with other social contexts.—Under similar laboratory conditions, the frequency of displaying was similar for both sexes and during all social contexts (12–22 displays / h; Table 2.3), except when males displayed at other males. Then male display rate increased more than 10-fold, especially when males were in close proximity of one another (228 displays / h).

Although both sexes used the same repertoire of type A, B, and C displays across all social contexts (Table 2.3), the use of the display types varied with sex and social context. Males used nearly equal proportions of all three display types when alone (i.e., nondirected context), but performed primarily C displays when signalling towards females and males at a distance. During close consexual encounters, however, males within biting distance increased the proportion of A and B displays. In contrast to males, females did not display when alone (i.e., advertisement context), used almost exclusively A and B displays towards males, largely performed C displays towards other females, and did not increase the use of A and B displays when approaching other females within biting distance.

The use of dewlap extension with displays also differed with sex and social context (Table 2.3). For males, dewlap extension almost always occurred during the nondirected context, towards females, and towards other males at a distance (Table 2.3). However, when males approached to within biting distance of other males, their dewlaps were rarely extended. In contrast to males, female dewlap extension was rare when signalling to males, but frequent when signalling other females. Females did not decrease dewlap use during close consexual encounters.

Displays were sequenced in volleys by both sexes, but volleys were used most frequently by males signalling females and other males at a distance (Table 2.3). The lowest proportion of volleyed displays was that of females towards males, and of males during close consexual encounters. Both sexes employed numerous modifiers during consexual displaying, and two signals appeared sex-specific. The shudderbob modifier seems restricted to male displays during heterosexual and non-directed contexts, and neckbending appears to be a female signal of sexual receptivity.

Discussion

During heterosexual interactions, both sexes performed the same three cadence patterns of type A, B, and C headbob displays (Fig. 2.1), and performed these displays with equal stereotypic precision (Table 2.1). This observation corrects the misconception introduced by prior studies (e.g., Crews, 1973b, 1975; Greenberg, 1977) that the displays of female *A. carolinensis* lack the distinct patterns and stereotypy typical of male displays. Furthermore, the A, B, and C display patterns performed during heterosexual interactions were virtually indistinguishable from the A, B, and C display patterns documented during other social contexts of *A. carolinensis*. Our analysis found little variance in display structure attributed to social context when comparing displays performed during heterosexual interactions with those reported by Jenssen et al. (2000) for consexual male and consexual female interactions (Figs. 2.2–2.4). That the sexes of *A. carolinensis* use the same A, B, and C headbob displays in different social contexts demonstrates why labelling displays with a functional epithet can be inappropriate. Functional labelling carries the presumption that rigorous testing has eliminated other possible functions for the physical signal. If the presumed function is incorrect, the label prevents or misleads further research and obscures evolutionary interpretations of a species' communication system (sensu Tinbergen, 1951).

To make informed inferences about the social functions and selective benefits associated with *A. carolinensis* displays, interpretations are best made within the context of the species' mating system and within a more natural social setting than that of our manipulated social contexts within enclosures. Fortunately, recent field studies have documented the pre-breeding, breeding, and post-breeding activity profiles of free-ranging *A. carolinensis*. These data provide a realistic description of the species' mating system and social organization (see Introduction). By integrating these field data with our observations on captive subjects, we can revisit our initial predictions and suggest likely functions for male and female signalling, and how signal use and recipient responses may affect male and female fitness.

Predictions

No courtship-specific displays.—Our first prediction was supported. The lack of courtship-specific signals is consistent with the species' mating system. Since both sexes disperse simultaneously from overwintering sites into the habitat prior to the onset of the breeding season (Jenssen et al., 2001), males and females are essentially within sight of one another as pre-reproductive neighbors. Thus, at the onset of reproduction, neither sex needs to search extensively for some distant mate nor attract distant mates with a long-distance signal. Furthermore, because females tend to be the passive sex in the *A. carolinensis* mating system (i.e., female-defence polygyny, see Introduction), field data suggest that male fitness is not dependent on the design of displays to attract females or influence female mating decisions (Nunez et al., 1997; Jenssen and Nunez, 1998). If female choice (i.e., intersexual selection) were influencing signal evolution in *A. carolinensis*, one would expect to find a courtship-unique male display, or at least some prominent modification to headbob displays used during courtship. However, the physical features of the three display types as performed by courting males are identical to those given in other social contexts.

The closest potential courtship-specific signal behaviour we observed for males were the shudderbobs that accompanied a fourth of male displays (Table 2.3, Fig. 2.5). Though some investigators have used shudderbobs (also called "rapid nods") as a criterion with which to identify "the courtship display" of captive male *A. carolinensis* (e.g., Greenberg and Crews, 1983), free-ranging males frequently perform displays that end in shudderbobs while advertising and patrolling their territory (Jenssen, unpublished field data). In addition, males of other lizard species are known to use the shudderbob modifier with their headbob displays during consexual and non-directed contexts, as well as during courtship (e.g., Jenssen, 1977; Jenssen and Rothblum, 1977; Ruby, 1977; Jenssen, 1979). That males of many species use shudderbobs in a variety of social contexts argues against this modifier being an exclusive signal for either *A. carolinensis* or the courtship context. More likely, shudderbobs might be an expression of general arousal. The only courtship-specific signal performed by females was the neck-bend posture. Neck-bends have been observed for both captive and free-ranging females of *A. carolinensis* (Crews, 1973a; Nunez et al., 1997) and occurs as a prelude to the precopulatory neck hold by males. The consistent co-occurrence of neck-bend and copulation reasonably implies that this posture is a sexual invitation by a receptive female.

Intrasexually selected display structure.—Our second prediction, that displays used during the heterosexual context should be similar in structure to displays used during non-directed and consexual contexts, was also supported. The type A, B, and C display patterns are essentially identical across all social contexts. Therefore, the question arises as to which social context, consexual (inference for intrasexual selection) or heterosexual (inference for intersexual selection), has most affected the design of the displays and the size of the display repertoire of *A. carolinensis*. The species' mating system (see Introduction) suggests that male fitness, and hence selection on male signal structure and use, is primarily affected by the outcome of inter-male aggression over access to females. Therefore, intrasexual selection on males should primarily influence signal traits, such that displaying confers an advantage to the signaller by facilitating the defence or takeover of territories. In contrast to males, female fitness seems little affected by the outcome of consexual female interactions (see Introduction). Thus, female signal traits should be less influenced by intrasexual selection than those of males. This premise predicts sexually dimorphic signal structure and/or use during consexual interactions, a prediction strongly supported by *A. carolinensis* during consexual contexts (Jenssen et al., 2000; Table 2.3).

From the design features of the displays of *A. carolinensis*, we can also infer the effects of intrasexual selection. Most obvious is the dewlap. For the average sized male, the area of the extended dewlap is extensive and seven-fold larger than that of the average sized female (1.52 cm^2 versus 0.22 cm^2; Jenssen et al., 2000). The large, sexually dimorphic male dewlap would effectively increase display broadcast distance over that of a female dewlap, an obvious benefit to males who continuously advertise and defend the boundaries of large territories (Jenssen et al., 1995). In addition, because dewlap size is an honest indicator of male body size (Jenssen et al., 2000) and relative body size of males usually predicts aggressive outcomes (Tokarz, 1985), a large dewlap may intimidate consexual rivals, especially where combatants use display modifiers (e.g., sagittal compression, gular expansion, raised crest; Table 2.3) to deceitfully appear large. For females, intrasexual selection for an enlarged dewlap as a feature designed for consexual contests would be unexpected given that neighboring females tolerate overlapping home ranges, infrequently interact, and do not advertise their lightly defended territories (Nunez et al., 1997; Jenssen and Nunez, 1998; Jenssen et al., 2000). The small dewlap of females reflects little selection for extended visibility or stimulus enhancement, regardless of possible signal function.

From the use and size of the display repertoire of *A. carolinensis*, we can infer further effects of intrasexual selection. Among the various social contexts, it is only during consexual encounters between adult males that all three display types are used with high frequency (Table 2.3). We suggest that this frequent use of all display types reflects the primary context in which multiple displays are most strongly selected. Inter-male contests involve ritualized sequences of behaviours in which the three display types are predictably orchestrated. Initially, males exchange displays at a distance, primarily using volleys of type C displays with dewlap extensions. The second stage involves approach and increased risk; now males proportionally increase type A and B displays, while infrequently signalling in volleys of displays and rarely extending their dewlaps. The final stage concludes with jaw sparring and jaw locking (e.g., Greenberg and Noble, 1944; DeCourcy and Jenssen, 1994; Table 2.3). By contrast, female-female contests lack the signal complexities and ritualization of male contests (Jenssen et al., 2000; Table 2.3), and resemble the social signalling of juveniles (Lovern, 2000; Table 2.3). Therefore, we suggest that *A. carolinensis* evolved a repertoire of multiple display types through the effects of intrasexual selection on males. Frequent and escalated inter-male contests that significantly influenced male fitness may have lead to the evolution of successive display types that would have functioned to bring a competitive edge to the signaller through some mechanism of intimidation (Jenssen, 1977, 1978; Ord et al., 2001). Supporting evidence for this evolutionary inference comes from a comparative study of lizard species, where male-biased sexual size dimorphism (an indicator of intrasexual selection) is significantly correlated with signal repertoire size (Ord et al., 2001).

Conversely, evidence for intersexual selection on the evolution of heterosexual displays is weak. First, there appears to be little opportunity for mate choice by female *A. carolinensis* during home range settlement (Jenssen et al., 2001), or after home ranges are established (Jenssen and Nunez, 1998). Second, attempts to experimentally demonstrate female mating preferences by *A. carolinensis* have been equivocal (Andrews, 1985b; MacDonald and Echternacht, 1991; review by Tokarz, 1995). Third, male signal use during heterosexual interactions, as an indicator of selection pressure, would also indicate little selective influence on signal evolution in *A. carolinensis*. Despite the three display types in their repertoire, males predominately used type C displays during interactions with females, and displayed four-fold less frequently and with shorter volleys than during consexual interactions (Table 2.3).

Sexually dimorphic display use.—Our third prediction was supported in a dramatic manner. Males and females used an antithetical pattern of signalling. First, males performed predominately type C displays (89%), whereas females performed mostly A and B displays (48% and 50%, respectively; Fig. 2.6, Table 2.3). Second, males extended the dewlap with almost all displays (98%), whereas females rarely extended the dewlap with displays (< 2%; Table 2.3). Third, males performed 80% of displays in volleys of two or more sequenced displays, whereas females performed only 12% of displays in volleys

(Table 2.3). Last, males concluded 22% of displays with shudderbobs, whereas females never used shudderbobs when displaying (Fig. 2.5, Table 2.3).

Sexual identification would be the most obvious function for the divergent signalling patterns of males and females. However, the degree of sexual dimorphic signalling seems overly redundant, and even imprecise. Consider, as a more parsimonious pattern to satisfy the primary criteria for mating (i.e., species and sexual identity), that both sexes could simply use one display type with dewlap extension. Species identification would be accomplished because any one of the display types is a stereotyped, species-specific signal shared by individuals and populations (Lovern et al., 1999), and sex identification would be unequivocally accomplished by extending the sexually size dimorphic dewlap (Jenssen et al., 2000). When displaying to females, males appear to follow this simple signalling pattern for species and sex identification by using the type C display with dewlap extension. However, females displaying to males use an antithetical and more complex approach to species and sex identification by using type A and B displays without dewlap extension. Female display usage confirms species identification, but the omission of an extended dewlap withholds a non-ambiguous signal for sex identification. We suggest that females diverge from an expected pattern of heterosexual signalling, using a more ambivalent system than that of males, because there may be a secondary benefit for females to do so.

Female mimicry hypothesis.—Based on reasonable, circumstantial evidence, we propose the following hypothesis. Demographically, three reproductive classes exist in the *A. carolinensis* mating system: large, conspicuously territorial males (i.e., displaying and moving frequently to advertise and defend their territory) that represent about a third of adult male population; adult females that reside within the patrol areas of territorial males; and smaller adult males that cannot successfully defend a territory containing females. Because most small males are inconspicuous, we have little field data on their activity patterns or signalling behaviour. However, we have captured small males near, and occasionally inside, the territories defended by larger territorial males, suggesting that some small males reside covertly near or within the territories of larger males. Further, Passek (2002) has identified through genetic testing that some offspring of resident females are fathered by small males residing within the territory of a larger male. Thus, by residing in close proximity to territorial males, “covert males” benefit by being in good habitat, close to mating opportunities, and in position to take over a territory if a territorial male disappears or becomes disabled. The cost of being covert would be detection, confrontation, and eviction by the more aggressive territorial male. However, this cost could be minimized if, when detected and signalled to by a territorial male, a covert male would signal ambiguously about its sexual identity. A covert male should be selected to: 1) avoid male-typical courtship signals (e.g., C displays); and, 2) never extend the dewlap, a sexual identity signal that cannot be faked. In contrast, territorial males should be selected to display their sex honestly (i.e., with dewlap extension) when approaching a conspecific of either sex, because there are no benefits to do otherwise.

If covert males gain some direct benefit (i.e., retaining residency) by signalling like females, then resident females should also receive an indirect benefit. Because mate selection by females is basically a passive process (i.e., neutral-mate-choice model, Jenssen et al., 2001), mating with covert males would provide a secondary source of sperm to females, and allow cryptic mate choice through sperm competition (Birkhead, 1998). An increasing number of studies show that even females in socially monogamous and polygynous mating systems may mate with multiple males. By doing so, females can receive direct benefits, such as increased nuptial resources and/or paternal investment (Thornhill, 1976; Soltis and McElreath, 2001), and/or indirect benefits, such as avoiding infertile sperm or genetic incompatibility, facilitating sperm competition, and increasing the viability, genetic diversity, and quality of offspring (Zeh and Zeh, 1996; Jennions and Petrie, 2000; Tregenza and Wedell, 2000).

In spite of the female-defense tactics of territorial males (Jenssen et al., 1995; Jenssen and Nunez, 1998), the life history traits of female *A. carolinensis* facilitate polyandry and sperm competition. Females store sperm up to seven months, repeatedly copulate 1-2 times per week, and lay single-egg clutches about every week for four months (Fox, 1963; Andrews, 1985a; Michaud, 1990; Nunez et al., 1997). However, the guarding behaviour of the territorial male limits resident female opportunity for extra-male copulations to two basic options. Females can either visit a neighboring male’s territory, or accept occasional copulations from small covert males that successfully avoid detection and eviction by the resident territorial male. The latter option is facilitated (i.e., indirectly selected) if females signal as they do, thus, permitting a directly selected mechanism (i.e., kleptogamy) for less-competitive covert males to gain mating opportunities through female mimicry.

Kleptogamy through female mimicry has been documented for small males in a variety of taxa, including insects (Forsyth and Alcock, 1990; Harari et al., 2000), fish (Ruchon et al., 1995; Goncalves et al., 1996; Oliveira and Almada, 1998; Uglem et al., 2001), birds (Hakkarainen et al., 1993; Saetre and Slagsvold, 1996; Langmore and Bennett, 1999), snakes (Mason and Crews, 1985; Shine et al., 2001), a salamander (Howard et al.,1997), and an *Anolis* lizard (Trivers, 1976). Although we lack direct field evidence to support our female mimicry hypothesis for *A. carolinensis* signal behaviour, we offer several observations from laboratory studies that are consistent with a hypothesis of sexual deception. First, captive males of *A. carolinensis* are known to engage in homosexual courtship and copulations (e.g., Noble and Bradley, 1933; Evans, 1938; Greenberg and Noble, 1944; Crews, 1973b; Cooper 1977), suggesting that there may be a degree of sexual misidentification and deception between males. Second, the signalling between paired males of *A. carolinensis* during laboratory studies also supports a hypothesis of sexual deception. When paired with a smaller male, the larger male performs headbob displays with dewlap extensions, while the smaller male performs displays without dewlap extensions (e.g., Crews, 1973b; 1975; Cooper, 1977; 1979; Sigmund, 1987). Unaware of the structural display types of *A. carolinensis*, past investigators interpreted and functionally labelled the signals of captive lizards in terms of social hierarchies (e.g., larger males were described as 'dominant' towards smaller 'subordinate' males, and displays given by females and small males without dewlap extension were termed "subordinate nodding"; Crews, 1975). However, these laboratory observations could also be interpreted as evoking our suggested adaptive signalling by territorial males (type C with dewlap extension) and females and covert males (type A and B without dewlap extension). Our female mimicry hypothesis for *A. carolinensis* could easily be tested by analyzing the display exchanges between female-sized males and larger males who are of territorial status. The protocol could include small-male introductions into the territories of free-ranging males, and into large enclosures containing complex habitat, females, and a large resident male.

Additional signal functions.

Species discrimination.—Each of the three display types of *A. carolinensis* is quite stereotypic, species-specific, and could certainly function as a species discrimination signal. Since Carpenter and Grubitz (1961) first quantified the headbob displays of lizards, most lizard species examined have been found to possess stereotypic and species-typical display cadence patterns (Carpenter, 1986). The idea that species-specific headbob displays serve as reproductive isolating mechanisms was quite strongly advanced for *Anolis* species because of the added nuance of species-typical dewlap colours among parapatric and sympatric congeners (e.g., Ruibal, 1967; Rand and Williams, 1970; Webster and Burns, 1973). However, experimental evidence for display signals as a criteria of species identification is lacking. Of the few studies that examined female preferences for males with conspecific displays and/or dewlap colour, only two studies supported a species discrimination function (e.g., Jenssen, 1970; Sigmund, 1978), while three others did not (e.g., Crews, 1975; MacDonald and Echternacht, 1991;

Jenssen, 1996). Some authors have suggested that male anoles may also use displays to discriminate conspecifics from sympatric cogeners during inter-male encounters (e.g., Ortiz and Jenssen, 1982; Losos, 1985; Macedonia and Stamps, 1994; Macedonia et al., 1994).

Selection for a species discrimination function for the display signals of *A. carolinensis* would be expected to be relaxed, however, because the species has been the only anole (disregarding recent exotic introductions in Florida) endemic to the continental United States for millions of years (Buth et al., 1980). Nonetheless, strong stabilizing selection on signal behaviour must occur because geographically disjunct populations of *A. carolinensis* (e.g., Georgia, Florida, and Hawaii) all share the same three species-specific display types with relatively minor inter-population differences (Lovern et al., 1999), despite an extensive mainland distribution (approximately 1.9 million km^2, McGeveran, 2002) that holds ample opportunity for alternative selective directions (e.g., varying habitat, predator pressure, and inter-deme isolation) or genetic drift on display phenotypes among local populations. In this study, we have argued that the number and structure of display types in the *A. carolinensis* repertoire reflect intrasexual selection (i.e., male fitness advanced through signaling during consexual activities), rather than intersexual selection (i.e., male fitness advanced through signaling during heterosexual activities). Since courtship-based selection is an unlikely explanation for the uniformity of male and female displays, we suspect that a stabilizing influence common to all populations of *A. carolinensis* may occur as a result of inter-male competition. However, the exact nature of this selection is currently unclear.

Individual discrimination.—Variation in headbob cadence patterns between different individuals could serve as a cue for individual recognition among displayers (e.g., Stamps and Barlow, 1973; Crews, 1975; Jenssen, 1971, 1977; Sigmund, 1978; Carpenter, 1982; Martins, 1991). We found that in spite of very stereotyped display performances, inter-subject differences among *A. carolinensis* displays were sufficient for discriminant statistical procedures to successfully assign most individual display performances to their respective displayer. However, because of the relatively small variance in display units, we do not consider that the displays, per se, are being selected for displayer identity. If displayers benefit by uniquely displaying in some manner to neighbors or mates (i.e., selection on the displayer), then display structure would show much greater inter-individual variation than intra-individual variation, and this prediction is not particularly supported (Fig. 2.4). If individual recognition occurs in *A. carolinensis*, and is mediated in part by display cadence patterns, then we suggest that the benefit of such recognition rests with the recipient of the display (i.e., selection on the recipient). Receivers would then be selected for perceptual acuity and learning of small variations in inter-display cadence, in conjunction with other traits, to discriminate among individuals. There is mounting evidence that some lizards, including *A. carolinensis*, can discriminate among individual conspecifics. As examples, males can discriminate between familiar mates and novel females (Cooper, 1985; Tokarz, 1992; Orrell and Jenssen, 1998; Orrell and Jenssen, 2002) and among neighboring males or prior male rivals (e.g., Qualls and Jaeger, 1991; Fox and Baird, 1992; Olsson, 1994; Whiting, 1999; Lopez and Martin, 2001). However, experimental evidence that individual recognition is being cued by display structure remains weak.

Overview.—We make three broad generalities for the display behaviour of *A. carolinensis*: 1) all social contexts are served by a common repertoire of the same three display types; 2) intrasexually selected processes appear to have the greatest influence on reproductive success and, by logical extension, on associated display structure and repertoire; and 3) the sexes use a divergent pattern of intersexual signalling that facilitates sex recognition, but also suggests a deceptive signalling strategy favouring an alternative mating strategy for both females and small males. Logically, these three generalizations should integrate with the species' social organization. To begin, the use of the same display types during both hetero- and consexual social contexts indicates that only one of these contexts has primarily influenced the uniform display cadence patterns and number of display types that occur across different kinds of social interactions. We infer from the species' female-defense polygynous mating system, that intrasexual selection appears to have the most effect on male reproductive success (i.e., as facilitated by male signalling traits) through the outcome of territorial contests. In addition, female reproductive success within this mating system appears to be disassociated from active mate choice, and thus from selection on male signalling traits. That mainland *A. carolinensis* has had no other sympatric congeners in recent geologic history diminishes another condition for intersexual selection; females need not be choosy about display traits of prospective mates to avoid outbreeding. Finally, we found a dimorphic pattern of heterosexual signalling: territorial males signalled their sexual identity in a parsimonious and unequivocal manner, while females used signals that were sexually ambiguous. This excessive divergence in female signalling stimulated our hypothesis of permissive female-mimicry, which represents a logical integration of female and small male fitness options within a mating system overtly controlled by large males. Without an understanding of the intersexual dynamics of the *A. carolinensis* mating system, our inferences for the sexually dimorphic signal pattern would have concluded with simple sexual identity.

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Table 2.1. Mean, standard error (SE), and coefficient of variation (CV) for display unit durations (units 1-11) and total display duration (Total; all units in a display, through unit 15) of A, B, and C displays performed by captive *Anolis carolinensis* during the heterosexual context. Intersexual comparisons were statistically insignificant at P < 0.001 (sequential Bonferroni method; Rice, 1989).

Display		Female Displays			Male Displays			Kruskal-Wallis tests	
Type	Unit	Mean (s)	SE	CV	Mean (s)	SE	CV	H	P
A	1	0.217	0.006	12.3	0.176	0.011	14.3	8.18	0.004
	2	0.106	0.008	32.6	0.112	0.026	52.9	0.04	0.845
	3	0.138	0.002	6.0	0.142	0.012	18.1	0.00	0.969
	4	0.185	0.010	21.8	0.139	0.017	27.7	4.00	0.046
	5	0.165	0.005	11.7	0.167	0.024	31.6	0.68	0.410
	6	0.338	0.016	19.4	0.337	0.052	34.7	0.01	0.906
	7	0.126	0.003	8.6	0.128	0.008	14.0	0.04	0.844
	8	0.087	0.004	20.8	0.076	0.006	18.0	1.88	0.170
	9	0.123	0.002	6.8	0.123	0.005	8.6	0.00	1.000
	10	0.192	0.007	15.6	0.160	0.033	46.5	0.67	0.411
	11	0.123	0.003	10.5	0.118	0.007	12.7	0.39	0.530
	Total	2.186	0.042	8.0	1.974	0.038	3.9	3.54	0.060
B	1	0.159	0.003	6.6	0.148	0.005	7.4	2.46	0.117
	2	0.166	0.012	30.3	0.151	0.007	10.6	0.61	0.433
	5	0.343	0.011	13.8	0.388	0.014	8.2	4.65	0.031
	6	0.245	0.014	24.2	0.298	0.014	10.6	2.71	0.100
	7	0.148	0.004	11.1	0.122	0.007	12.0	5.72	0.017
	8	0.082	0.004	19.3	0.084	0.005	12.7	0.00	1.000
	9	0.144	0.003	8.2	0.131	0.009	15.1	3.12	0.077
	10	0.281	0.010	15.1	0.261	0.022	19.2	0.26	0.611
	11	0.147	0.004	12.0	0.137	0.007	11.1	0.96	0.327
	Total	2.107	0.045	8.9	1.986	0.034	3.9	1.12	0.290

Table 2.1 (continued). Mean, standard error (SE), and coefficient of variation (CV) for display unit durations (units 1-11) and total display duration (Total; all units in a display, through unit 15) of A, B, and C displays performed by captive *Anolis carolinensis* during the heterosexual context. Intersexual comparisons were statistically insignificant at $P < 0.001$ (sequential Bonferroni method; Rice, 1989).

Display		Female Displays			Male Displays			Kruskal-Wallis tests	
Type	Unit	Mean (s)	SE	CV	Mean (s)	SE	CV	H	P
C	5	0.452	0.028	12.4	0.516	0.023	10.1	2.16	0.142
	6	0.265	0.019	14.4	0.198	0.037	42.2	1.51	0.219
	7	0.157	0.008	10.5	0.146	0.006	9.1	0.56	0.455
	8	0.204	0.015	14.3	0.192	0.007	7.9	0.54	0.462
	9	0.169	0.022	25.7	0.178	0.005	6.7	1.50	0.221
	10	0.176	0.013	15.3	0.183	0.014	16.6	0.00	1.000
	11	0.124	0.008	13.3	0.127	0.002	3.6	0.29	0.592
	Total	2.144	0.038	3.5	2.005	0.059	6.6	2.16	0.142

Table 2.2. Mean and coefficient of variation (CV) of bob and pause units for A, B, and C displays performed by male and female *Anolis carolinensis* during heterosexual and consexual contexts. Stereotypy was examined among subjects (CVs calculated using within-subject mean unit durations as values) and within subjects (CVs calculated for each subject separately). Asterisks (*) indicate statistically significant comparisons of bob and pause unit stereotypy (using Kruskal-Wallis Tests and the sequential Bonferroni method; Rice, 1989).

			Among-subject stereotypy					Within-subject stereotypy				
			Mean, CV			Kruskal-Wallis		Mean, CV			Kruskal-Wallis	
Context	Sex	Type	Bobs	Pauses	N	H	P	Bobs	Pauses	N	H	P
Hetero-sexual	M	A	9.1	20.9	7, 6	9.0	0.003*	13.2	16.8	119, 102	2.7	0.101
		B	10.2	21.4	6, 5	7.5	0.006*	11.3	15.0	102, 85	3.6	0.057
		C	16.8	16.0	5, 4	0.2	0.624	9.6	12.0	10, 8	0.5	0.473
	F	A	6.9	32.4	7, 6	4.0	0.046	17.1	25.3	28, 24	3.4	0.065
		B	12.9	13.7	6, 5	0.3	0.584	12.0	15.9	30, 25	1.6	0.207
		C	6.4	20.4	5, 4	3.8	0.050	16.2	19.0	20, 25	0.0	0.945
	Pooled		12.1	21.3	36, 30	21.0	0.0001*	12.9	17.0	314, 264	9.5	0.002*
Con-sexual	M	A	16.2	41.2	5, 5	4.8	0.028	8.0	2.0	5, 5	2.0	0.156
		B	9.0	24.0	4, 4	4.1	0.043	10.7	22.3	16, 15	1.3	0.251
		C	13.8	31.3	3, 3	3.9	0.049	11.9	18.9	40, 40	14.3	0.0002*
	F	A	10.7	21.5	5, 5	4.8	0.028	9.9	13.3	40, 40	0.2	0.690
		B	11.5	25.0	4, 4	5.3	0.021	11.8	18.9	28, 28	0.3	0.555
		C	9.3	20.1	3, 3	3.9	0.049	16.3	29.8	24, 24	8.0	0.005*
	Pooled		11.9	27.7	24, 24	23.7	0.0001*	11.8	19.2	152, 151	13.7	0.0002*

Table 2.3. Comparison of signal use by *Anolis carolinensis* during heterosexual (male-female), consexual (male-male, female-female), non-directed (male-alone, female-alone), and conspecific juvenile social contexts. Signal use during consexual contexts is for distant (>60 cm) and close (<20 cm) inter-subject separation distances.

Signal	Heterosexual Context		Consexual Context				Non-directed Context		Conspecific
Traits	Males	Females	Males[1, 2]		Females[3]		Males[1]	Females[2]	Juveniles[6]
			>60 cm	<20 cm	>60 cm	<20 cm			
Proportion of display types (A:B:C)	1:1:16	24:25:1	1:1:18	5:7:8	1:3:16	2:3:15	1:3:3	–	1:1:9*
Display rate (per h)	19	22	84	228	18	12	18	–	3-14*
Displays in volleys	80%	12%	80%	8%	73%	47%	46%	–	not examined
Displays w/dewlap	99%	<2%	86%	15%	49%	41%	97%	–	56%*
Volley length	2.5	2.3	4.2	3.0	3.0	2.8	2.7	–	not examined
Static display modifiers[4]	No	No	Yes	Yes	Yes	Yes	No	–	Yes
Displays with shudderbobs	22%	0	not examined		0	0	Yes[5]	–	not examined
Neck-bend	No	Yes	No	No	No	No	No	–	No

[1] DeCourcy and Jenssen, 1994

[2] DeCourcy, 1991

[3] Jenssen et al., 2000

[4] Static display modifiers: sagittal compression, gular expansion, raised crest, mouth gape (descriptions in Jenssen, 1979)

[5] Jenssen, unpublished field data

[6] Lovern, 2000

*Juveniles had significant ontogenetic shifts in signal use as they grew larger in body size.

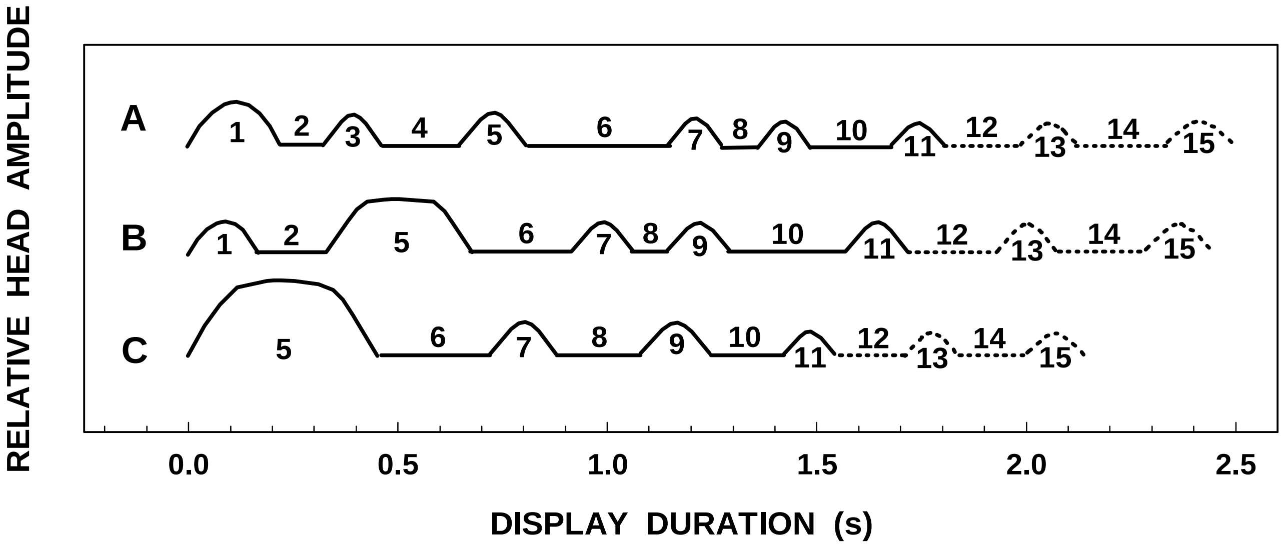

Figure 2.1. Display Action Pattern (DAP) graphed representations of type A, B, and C displays of captive *Anolis carolinensis* during the heterosexual context, with relative head amplitude plotted over time. Odd numbers label the bob units, even numbers label the inter-bob pause units, solid lines indicate core units, and broken lines indicate optional units.

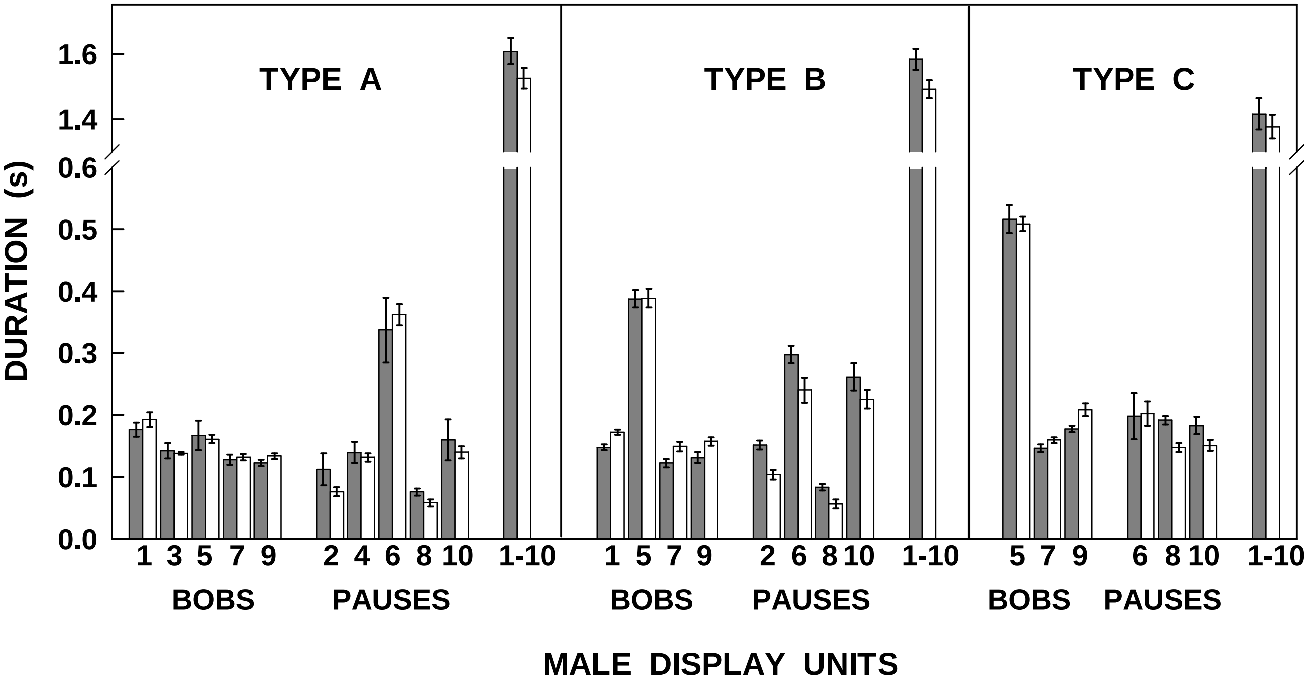

Figure 2.2. Comparison of the mean unit durations (±SE) of type A, B and C displays performed by captive male *Anolis carolinensis* during heterosexual (■) and consexual (□) contexts (within-subject means used as variables). None of the units compared were significantly different between contexts (Kruskal-Wallis tests, P > 0.002; sequential Bonferroni adjusted P-values). Sample sizes for the heterosexual context included 31 type A, 29 type B, and 66 type C displays performed by 5 males, and for the consexual context included 47 type A, 49 type B, and 76 type C displays performed by 8 males.

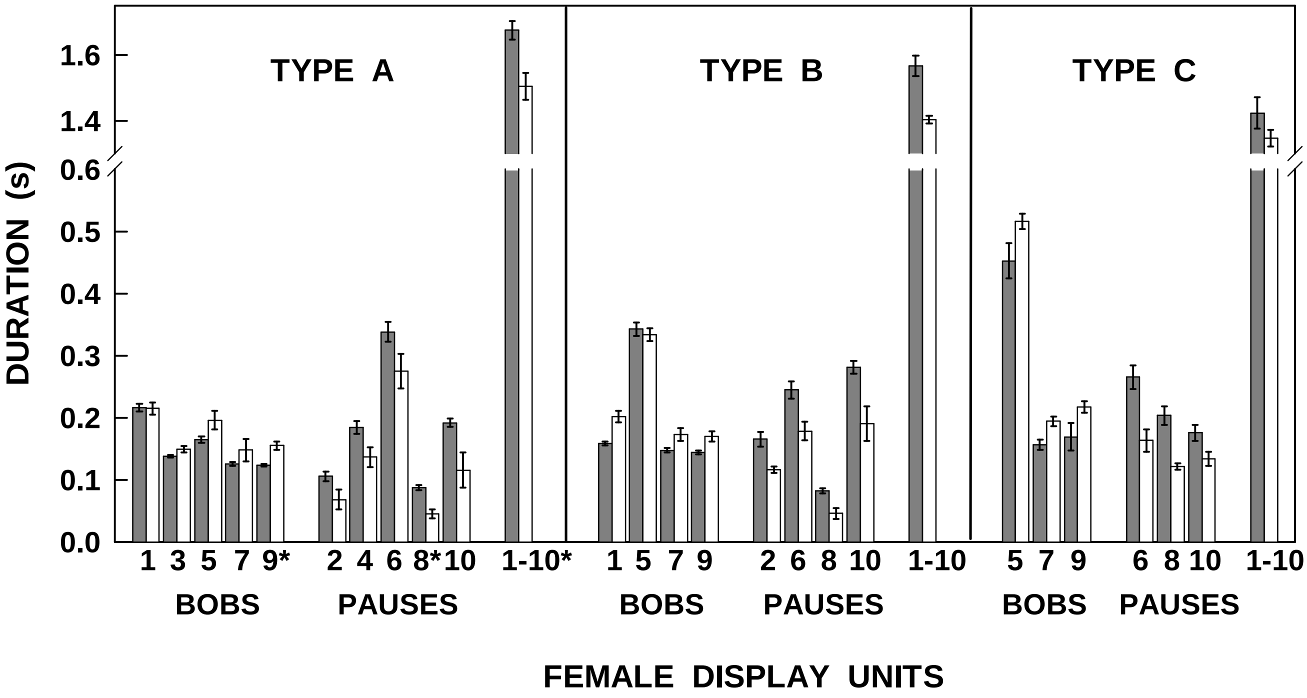

Figure 2.3. Comparison of the mean unit durations (±SE) of type A, B and C displays performed by captive female *Anolis carolinensis* during heterosexual (■) and consexual (□) contexts (within-subject means used as variables). Units marked with an asterisk (*) were significantly different between contexts (Kruskal-Wallis tests and sequential Bonferroni adjusted P-values). Sample sizes for the heterosexual context included 163 type A, 165 type B, and 7 type C displays performed by 17 females, and for the consexual context included 7 type A, 20 type B, and 105 type C displays performed by 16 females.

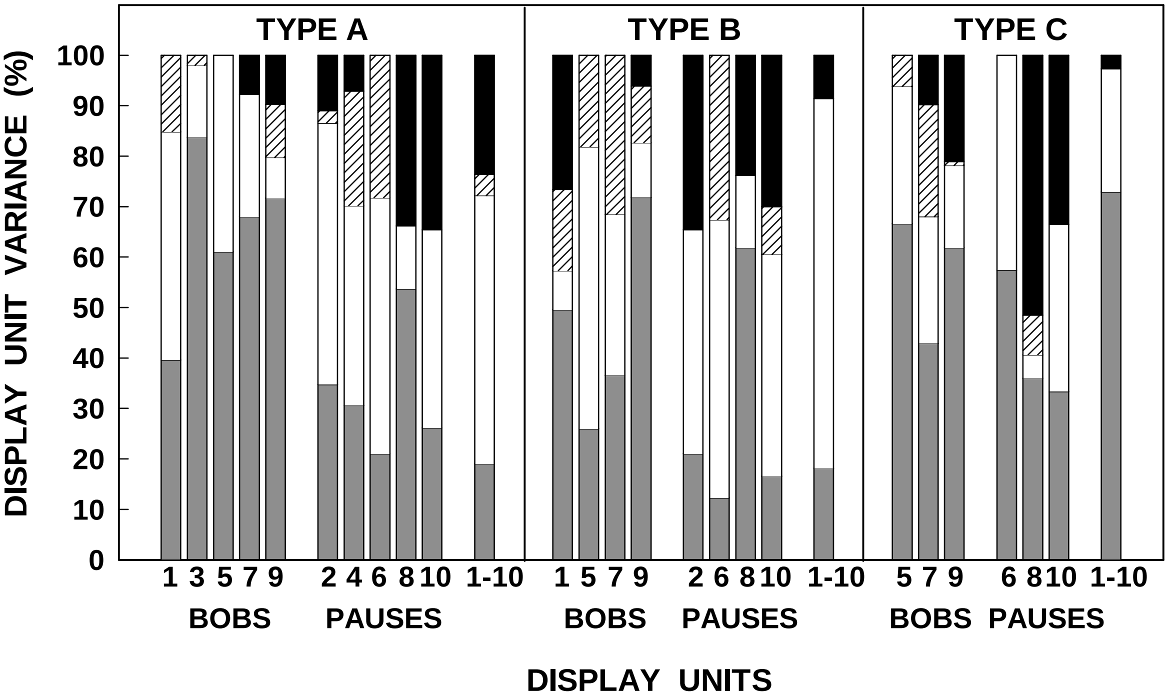

Figure 2.4. Proportion of variance found in the unit durations of captive *Anolis carolinensis* type A, B and C displays attributed to context (■), sex (▨), among-subject (☐), and within-subject (▩) components by a nested analysis of variance. Sample sizes for the heterosexual context included 163 type A, 165 type B, and 7 type C displays performed by 17 females, and 31 type A, 29 type B, and 66 type C displays performed by 5 males. Sample sizes for the consexual context included 7 type A, 20 type B, and 105 type C displays performed by 16 females, and 47 type A, 49 type B, and 76 type C displays performed by 8 males.

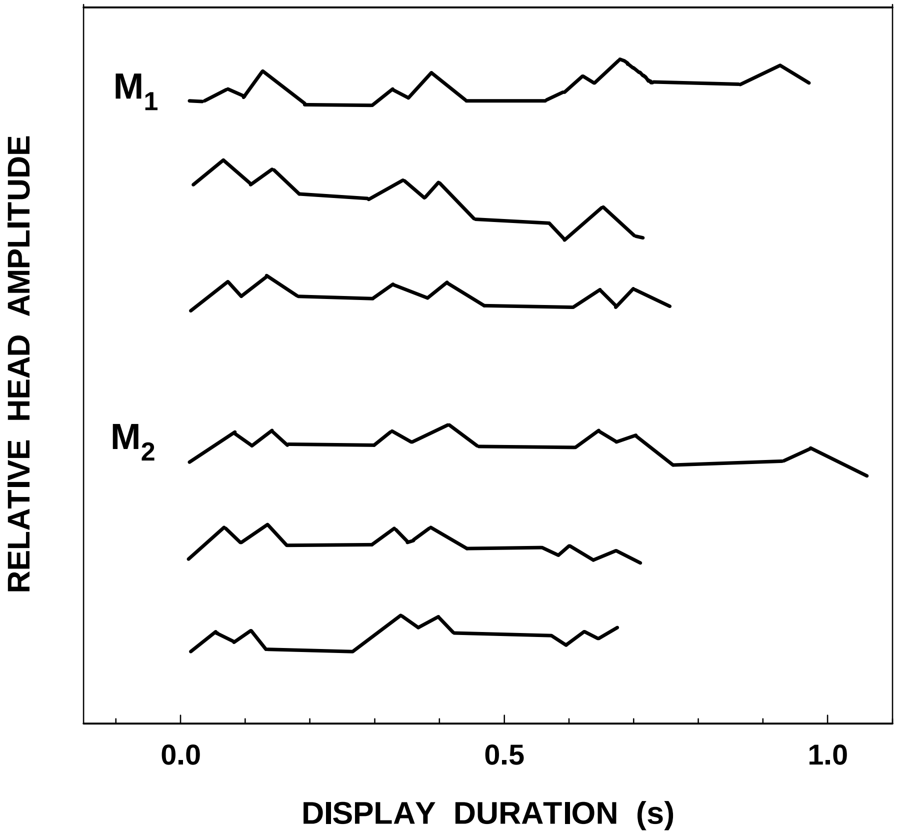

Figure 2.5. Display Action Pattern (DAP) graphed representations of shudderbobs performed by two captive male *Anolis carolinensis* (M1 and M2).

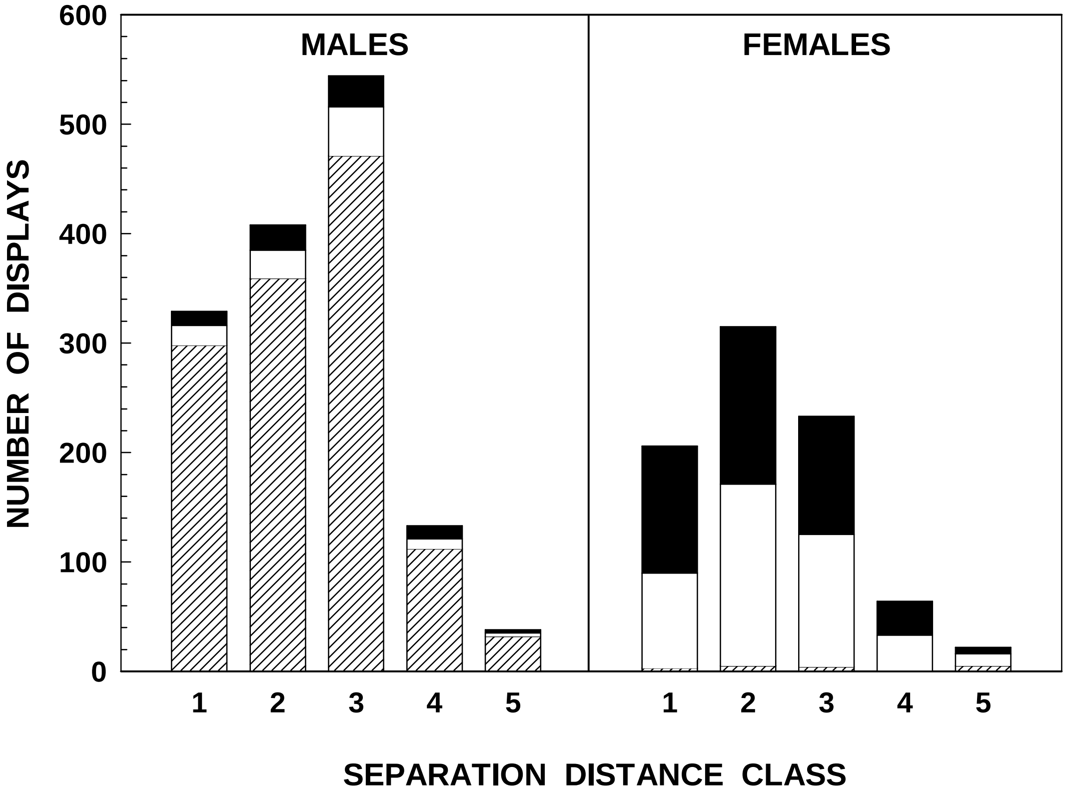

Figure 2.6. The number of type A (■), B (□), and C (▨) display patterns performed by 17 male and 17 female captive *Anolis carolinensis* divided into the following five classes of separation distance: (1) 0-20 cm, (2) 21-40 cm, (3) 41-60 cm, (4) 61-80 cm, and (5) >80 cm.

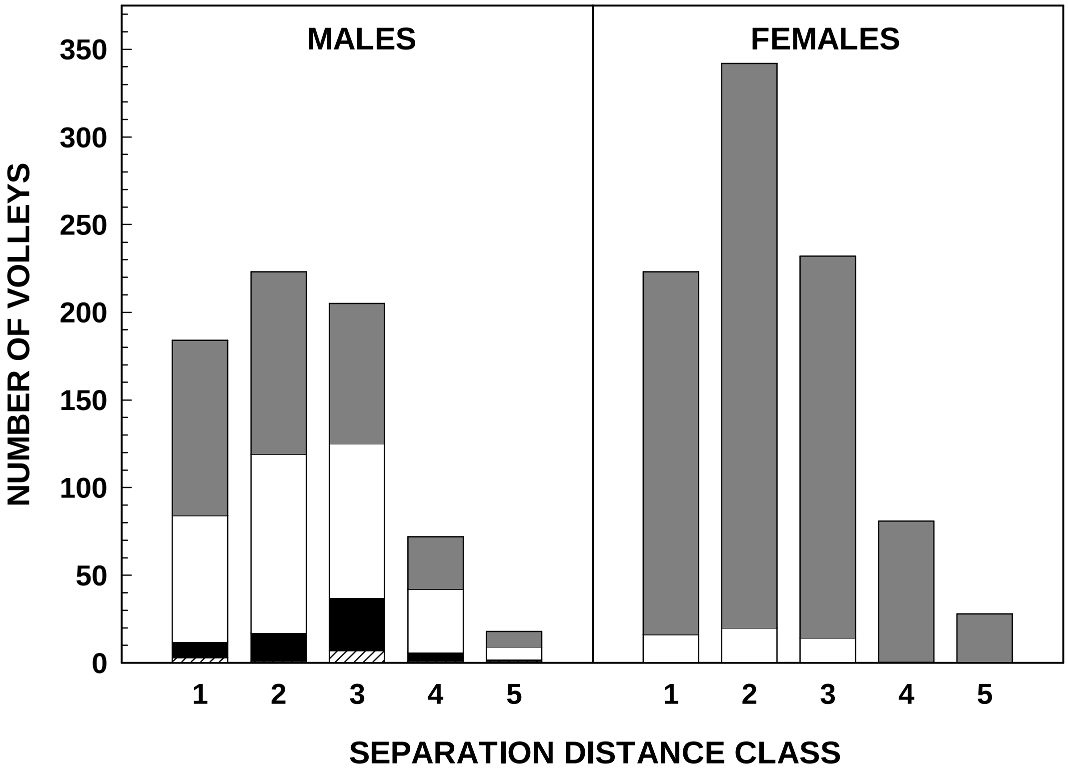

Figure 2.7. The number of single displays (▩) and number of volleys of sequenced displays (volley of 2-4 displays - ☐, volley of 5-7 displays - ■, volley of 8-17 displays - ▨) performed by 17 male and 17 female captive *Anolis carolinensis* at each of the following five classes of separation distance: (1) 0-20 cm, (2) 21-40 cm, (3) 41-60 cm, (4) 61-80 cm, and (5) >80 cm.

CHAPTER 3

Male mate choice by the polygynous lizard, *Anolis carolinensis*: a preference for novel females

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Abstract

Laboratory and field manipulations tested whether male *Anolis carolinensis* lizards exhibit discrimination and preference for novel females over resident females. In 16 laboratory trials, we videotaped social interactions between paired males and females during baseline session (male and resident female housed together 1-3 weeks), resident-female session (male and reintroduced resident female), and novel-female session (male and novel female with resident female removed). We examined 22 behavioural variables. Male behaviours did not significantly differ between baseline and resident-female sessions, nor did female behaviours significantly differ among baseline, resident-female, and novel-female sessions. However, between resident-female and novel-female sessions, males significantly increased display rate (320%), volleys of repetitive displaying (300%), and volley length (150%), and significantly decreased the distance (375%) and number (430%) of movements traveled away from the female. We concluded that males discriminate novel females from resident females independently of female behavioural or chemical cues. In each of 18 field trials, we first videotaped baseline social interactions of the resident male and females in a naturally occurring, polygynous, breeding group. The next day, we released two novel females into the territory (so at least one female remained) and videotaped subsequent social interactions. In comparison to baseline observations, males significantly increased the proportion of time spent in female-directed activities (from 5% toward resident females to 53% toward the novel female) and the proportion of displays directed toward novel females (from 6% toward resident females to 51% toward the novel female), and significantly decreased the proportion of time spent in territorial activities (from 75% to 19%) and the proportion of displays used in territorial activities (from 94% to 44%). Data from both experiments indicate that males appear to distinguish among individual females, and use this ability to increase reproductive success by identifying and preferentially pursuing novel females over previously inseminated resident females. From the perspective of cognitive ethology, we suggest a model by which males control mating decisions within their territories.

Introduction

Within a polygynous mating system, males can maximize reproductive success by monopolizing females through inter-male contests or by participating in some form of mate choice. Although mate choice is traditionally associated with female-controlled mating systems, males should also exhibit mating preferences whenever the reproductive benefits outweigh the costs of being choosy (Trivers 1972; Parker 1983). The type of mate choice strategy most frequently studied is quality-based discrimination, in which individuals increase reproductive success by choosing a mate that would produce greater numbers of offspring or higher quality offspring (reviewed in Andersson 1994). Quality-based male mate choice has been documented for species in which fecundity is positively correlated with female body size (McLain & Boromisa 1987; Verrell 1989; Olsson 1993), species with female-biased operational sex ratios (Lawrence 1986; Colwell & Oring 1988; Kvarnemo & Ahnesjo 1996), and species in which males provide the bulk of parental care (Gwynne 1981; Berglund & Rosenqvist 1993).

Another male-initiated mate choice strategy, classically labeled the “Coolidge effect” (e.g., Dewsbury 1981), is characterized by an intense sexual interest in novel females. Males exhibiting a preference for courting and mating with a novel female versus a familiar female (i.e., a previously mated female) could increase their reproductive success by inseminating more females. A preference for novel females (hereafter termed PNF) requires that males either individually or categorically discriminate among females previously inseminated from those representing new mating opportunities. If males can discriminate among females, a PNF response would be expected for many mating systems, and especially for polygynous systems in which males are emancipated from parental care. Exceptions might be species in which mating with novel females results in reproductive penalties for males, such as some genetically monogamous species with biparental care requirements (e.g., Getz 1978; Thomas and Birney 1979), or monogamous species in which males guard and follow mates closely to prevent them from copulating with other males (e.g., Bull et al. 1998; Olsson and Shine 1998). Despite the logical presumption that many males should practice some type of mate choice (e.g., PNF), testing the phenomenon among taxa and mating systems has been limited (e.g., mammals, review by Dewsbury 1981; a salamander, Donovan & Verrell 1991; and four species of lizards: *Holbrookia propinqua*, Cooper 1985; *Anolis sagrei*, Tokarz 1992; *Eumeces laticeps,* Cooper 1996; *Eublepharis macularius*, Steele & Cooper 1997).

We examined male mate choice in the polygynous lizard, *Anolis carolinensis*, because its life history and ecological features predict a PNF response. First, neonates are precocial and independent of parental care. Without parental care constraints, adult males may not incur major reproductive penalties by increasing the number of mates. Second, females can store sperm for at least seven months (Fox 1963; Conner & Crews 1980). Given that females lay single-egg clutches at about weekly intervals (Andrews 1985; Michaud 1990) for four months (Ruby 1984; Jenssen & Nunez 1998), a male copulating once with a novel female could potentially fertilize up to 16 eggs. Third, because females tend to be clumped in stable, small, and overlapping home ranges (Jenssen & Nunez 1998), the most aggressive males establish long-term territories around multiple mates (Ruby 1984; Jenssen & Nunez 1998). With this association of reproductive females in space and time, a territorial male has the opportunity to become familiar with resident females. Given the above attributes of *A. carolinensis*, we would expect selection for a PNF response if: 1) a male can distinguish a new female in his area from a resident with whom he has been mating; and 2) if male reproductive success is positively correlated with the number of mates. Alternatively, if males cannot distinguish among females, or if the reproductive success of a male is more dependent on guarding females from other males than on mating with additional females, then selection should not favor the PNF response in male *A. carolinensis*.

To test for the PNF response in *A. carolinensis* males, we performed both laboratory and field experiments. Under laboratory conditions, we used male courtship responses toward introduced resident and novel females as a bioassay to distinguish among the following working hypotheses:

H_1, males do not differentially respond to females, and either lack the ability to discriminate among them and/or have no preferences;

H_2, males differentially respond to females, and prefer females based on factors other than resident or novel status (e.g., female body size or behaviour);

H_3, males differentially respond to resident and novel females, and prefer resident females;

H_4, males differentially respond to resident and novel females, and prefer novel females.

Under field conditions, we attempted to create realistic introductions of novel females into natural breeding groups of polygynous males and their resident females. Our objective was to document the responses of free-ranging males toward their resident females and introduced novel females to both validate the laboratory results and describe the full expression of PNF within a natural setting.

Methods

Laboratory Experiment

Sixteen adult males and 19 adult females (mean ± SD snout-vent lengths of 59.3 ± 6.9 mm and 50.5 ± 4.7 mm, respectively, and body masses of 6.2 ± 2.1 g and 3.9 ± 1.0 g, respectively) were collected early in the 4-month breeding season near Aiken, South Carolina, and brought to our laboratory at Virginia Tech. Lizards were housed in male/female pairs in 0.6 H x 0.6 W x 0.7 L m cages for 1-3 weeks prior to experimental manipulation; this time period insured sufficient time to establish that individuals of a pair were familiar with each other. Each cage was provided with branches, artificial plants, and peat moss substrate to simulate a natural habitat. Food (vitamin dusted crickets) and water (in dishes and by misting) were replenished every day. Cages were illuminated by two fluorescent (40 W) bulbs and one incandescent floodlight (150 W), providing 200-300 lux (LI-COR LI-185B photometer) on a 12L:12D cycle. Inside the cages, the light cycle temperatures ranged from 28ºC to a maximum of 42ºC directly under the flood lights, and about 24ºC during the dark cycle.

Experiments took place in a plywood observation enclosure (0.5 H x 0.7 W x 1.2 L m), with a screen top, glass front, habitat, and lighting as described above. The glass front was slanted and covered on the inside with nylon window screen to minimize the chance that subjects might respond to their own reflections. Because females were to be introduced into the observation enclosure as part of the experimental protocol, an opaque release box (8 x 5 x 10 cm) was built onto one end of the enclosure. The release box was opened by a remotely controlled sliding gate, through which an introduced female could enter the enclosure of her own volition. Introducing females into the observation enclosure through the release box eliminated an observer effect on the male subjects in the enclosure.

Pairs of subjects were videotaped from a darkened blind 1.5 m from the observation enclosure. Two video cameras (Panasonic WV-1550) mounted with 16-160 mm zoom lenses were operated by two observers, and one camera followed each lizard. The two video images were juxtaposed by a split screen generator (Vicon Model V270SPP8), recorded at 30 frames/s on a VCR (Panasonic Model AG-1950), and imprinted with elapsed time in 0.01s increments from a time-date generator (Odetics Model G-77). The videotapes were reviewed frame-by-frame to track 22 variables (Table 3.1). These variables were used to detect any differential responses of males and females to treatment effects.

The experimental protocol for each of 16 videotaped trials consisted of three sessions: 1) a baseline session of a resident male and female; 2) a resident female introduction session; and 3) a novel female introduction session. Each trial required five days. On the first day of a trial, a resident male/female pair were moved to the observation enclosure and left to acclimate to the new enclosure for three days. On the fourth day of a trial, we videotaped baseline behaviours of the resident pair for 30 min (baseline session), and then removed the resident female from the observation enclosure. Next, we randomly selected either the resident female or a novel female and placed her into the release box. After 15 min, the release box was opened remotely and the female entered the observation enclosure. We then recorded 60 min of either a resident-female or novel-female session, depending on which female had been selected. On the fifth day of a trial, a second 30 min baseline session and the remaining reciprocal 60 min session (either resident-female or novel-female) were videotaped. When the novel-female session was recorded first in a trial, the novel females were removed immediately after their sessions and the resident female was returned to the enclosure.

In all trials the introduced novel female had not previously associated with the tested male. We attempted to minimize the size differential between the novel and resident females in a trial (mean size difference = 5.2 ± 3.9 mm). From a pool of 19 females, 14 individuals were utilized as both a resident and a novel female in separate trials held at least one week apart. We randomized whether a female first served as a re-introduced resident or as an introduced novel female. By using females in both a resident and novel female capacity, we were able to test whether resident or novel status had an influence on individual female behaviour.

Field Experiment

The response of free-ranging males to novel females was tested in a riparian habitat along the Augusta Canal near Augusta, GA, during May - July, 1993. Novel females were introduced into the territories of males that had two or more resident females. Each introduction was conducted by two observers. One person directly videotaped (Panasonic AG-460 camera) the behaviour of the resident male. The other person used 10X binoculars to follow the novel female, and to dictate the behaviour and position of the female as a running commentary onto the audio track of the videotape. The videotapes were reviewed frame by frame to track 17 variables (Table 3.1).

Females used for introductions were collected > 200 m from where they were released in a trial to insure that they were previously unknown to the tested male. We distinguished novel females from resident females by noting unique natural markings of the novel female (e.g., a regrown or bent tail, or characteristic scar), or by applying a small spot of acrylic paint on the neck or tip of the tail. Resident males and females were not marked, captured or handled to minimize possible behavioural reactions to observers (e.g., Marcellini and Jenssen 1991). We addressed whether paint marking might facilitate novel female recognition by resident males by comparing male responses toward painted and unpainted novel females.

Eighteen trials were conducted, with each trial consisting of two sessions: 1) a baseline session of the resident male and females, and 2) a novel female introduction into the territory of the resident male. Each trial required two days. On the first day of a trial, the baseline session began when the resident lizards became active (~0900) and consisted of 1-2 h of videotaped resident male behaviour, including any interactions with resident females. On the second day of a trial, the novel-female session was created by introducing two novel females into the resident male's territory about 30 min before the local lizards usually became active (?0830). Two novel females were released because the large volume of male territories (69 m^3; Jenssen & Nunez 1998) permitted introduced females to hide for the duration of a trial, or to leave the territory before detection. In fact, both introduced females left the male's territory in 10 trials, necessitating the introduction of an additional female. The early morning release permitted the introduced females some time to adjust to their new surroundings before being seen and approached by a resident lizard. To minimize handling effects on novel females and possible disturbance to resident lizards, females were introduced into territories with a remotely-opened release box (4.0 H X 7.5 W X 8.0 L cm) attached to a 3 m pole. The novel-female sessions began with the presence of a novel female and the appearance of the resident male, and were videotaped for 1-2 h.

Ethical note: all lizards used in the laboratory study survived the experiment, and were released back into the field at the end of the study. In the field study, all novel females released into the territories of resident lizards also survived the experiment, and were allowed to remain in the field after their release.

Statistical Analysis

Variables were analyzed using descriptive statistics (mean, standard error, range), Wilcoxon signed-rank, Wilcoxon rank sum, and stepwise regression procedures (SAS version 6.12, SAS Institute Inc. 1989). The P-values from individual signed rank comparisons within a group of variables (i.e., P-values from tests addressing a common hypothesis) were evaluated using sequential Bonferroni adjustments to reduce possible type I errors (Rice 1989). To evaluate signed rank comparisons resulting in nonsignificant P values, and thus the possibility of making type II errors by incorrectly accepting the null hypotheses, we calculated the minimum detectable effect for each variable at a power level of 90% (Zar 1984; Thomas 1997; Hoenig & Heisey 2001). We considered that a detectable effect size of 200% was sufficient for identifying major changes in behaviour. Statistical tests were two-tailed, with an overall a = 0.05.

Results

Laboratory Experiment

Female Comparisons

For each trial, data from the two 30 min baseline sessions (one recorded prior to the resident-female session, one recorded prior to the novel-female session) were combined into a 60 min baseline session for comparison to resident-female sessions. Comparisons between baseline and resident-female sessions (Table 3.2) indicated that none of the 17 behavioural variables for females significantly differed (Wilcoxon signed-rank, T ranged -26.5 to 20, $N = 16$, NS; minimum detectable effect in 13 of 17 variables was < 200%). The lack of substantive differences in each female's behaviour between baseline and resident-female sessions suggests that the experimental procedure of handling, placement in the release box, the 15 min waiting period in the release box, and reentry from the release box, had a relatively minimal effect on female behaviour.

We then compared the behaviours of individual females to determine whether they behaved differently in their capacities as a novel or resident female. In comparing the behaviours of individual females between resident-female and novel-female sessions, we found that none of the variables (Table 3.2) significantly differed (Wilcoxon signed-rank, T ranged -20.5 to 26.5, $N = 14$, NS; minimum detectable effect in 13 of 17 variables was < 200%). Thus, individual females appeared to be relatively unaffected by their status as a resident or novel female.

We next compared behaviours of the resident and novel females within each trial to determine if behavioural differences in the individual pairs of females might have influenced a male's responses. For example, if the novel female displayed more frequently than the resident female, the male may also display more frequently to the novel female by responding in kind, and not necessarily as an indication of interest. Following sequential Bonferroni adjustments to the P-values, none of the 17 variables examined significantly differed between resident and novel females (Wilcoxon signed-rank, T ranged -44 to 40.5, N = 16, NS; minimum detectable effect in 11 of 17 variables was < 200%; Table 3.2). However, there was a tendency for novel females to move away from males more frequently and to greater distances than resident females, while resident females moved greater distances toward the male than novel females.

Females used display behaviours with similar frequencies during resident-female and novel-female sessions (Table 3.2). Female headbob display rates were about 20 displays/h, regardless of the type of session or the display rate of males. Females tended to perform mostly single displays (88% of displays), and though seven of 18 females occasionally performed displays in short volleys (mean size of 2.3 displays/volley, N = 51 volleys) volleys were not associated with any type of session. Females did not use postural modifiers (e.g., crest, lateral compression, gular expansion) and infrequently used behaviours that might relate to pheromone deposition (e.g., mouth wipes and body drags) and pheromone detection (e.g., lip smacks and substrate licks; Table 3.2).

Male Comparisons

For each trial, data from the two 30 min baseline sessions were combined into a 60 min baseline session for comparison to resident-female sessions. Comparisons between baseline and resident-female sessions indicated that none of the 22 behavioural variables significantly differed (Wilcoxon signed-rank, T ranged from -20 to 7, N = 16, NS; minimum detectable effect in 17 of 22 variables was < 200%; Table 3.3). The similarity of each male's behaviour between baseline and resident-female sessions suggests that the brief absence and reappearance of resident females neither stimulated nor inhibited male interest in their resident females.

Comparisons between resident-female and novel-female sessions, however, showed that five of the 22 male variables significantly differed (following sequential Bonferroni adjustments to P-values), with 14 of the 16 males exhibiting intensified courtship toward a novel female. Males displayed about three-fold more often in novel-female sessions than in resident-female sessions (64 versus 20 displays/h, respectively, Wilcoxon signed-rank, $T = -57$, $N = 16$, $P = 0.0016$; Table 3.3). The high display rate of males toward novel females was not a result of exchanging displays with novel females because resident and novel females had similar display rates, and novel females responded less frequently to the displaying of males than did resident females. Over half of male displays during novel-female sessions were performed with no response from novel females (33.4 displays out of the total 64.3 displays performed/h; Table 3.3), while less than a third of male displays during resident-female sessions were performed with no response from resident females (5.9 displays out of the total 20.0 displays performed/h, Table 3.3).

Males performed significantly longer and more frequent display volleys (defined as 2 or more displays < 2 s apart) during novel-female sessions than during resident-female sessions, averaging 3.7 versus 2.5 displays/volley, respectively (Wilcoxon signed-rank, $T = -33$, $N = 16$, $P = 0.001$), and 17.9 versus 6.0 volleys/h, respectively ($T = -36$, $N = 16$, $P = 0.0024$; Table 3.3). Because males also performed more single displays during novel-female sessions, the proportion of volleyed displays to total displays was about the same for both resident-female and novel-female sessions (mean proportion of volleyed displays was 66.4 ±20.6 and 68.8 ±35.3, respectively; $T = -23$, $N = 16$, NS, minimum detectable effect of 47%). Male display modifiers common to aggressive interactions (i.e, raised crest, lateral compression, gular expansion) rarely occurred during baseline, resident-female or novel-female sessions (Table 3.3). When display modifiers were used by males, the frequency of appearance for all modifiers combined was nearly 15-fold greater in novel-female sessions (2.9 modifiers/h) than in resident-female sessions (0.2 modifiers/h, respectively), although this difference was statistically insignificant following sequential Bonferroni P-value adjustment ($T = -14$, $N = 16$, NS, minimum detectable effect > 200%; Table 3.3).

Males moved twice as frequently and twice the distance toward novel females as toward resident females (respective Wilcoxon signed-rank statistics: $T = -51$ and -47, $N = 16$, $P = 0.006$ and 0.013), and were one fourth as likely to move away from novel females as from resident females (for number of moves and distance moved, $T = 51.1$ and 69, $N = 16$, $P = 0.002$ and 0.0007, respectively; Table 3.3). Persistent movements of males toward novel females and less movement made away from novel females as compared to resident females, suggests a greater interest in novel females than in resident females.

Male variables that had no significant differences between resident-female and novel-female sessions were: the proportion of displays accompanied by dewlap extension (98%), the proportion of displays terminated with shudderbobs (30%), the hourly rate of independent dewlap pulses (i.e., not associated with headbob displays; 0.3), and the hourly rate of body colour changes (0.5), lip smacks (3.4), substrate licks (2.6), mouthwipes (0.5), and body drags (0.2; Table 3.3)(Wilcoxon signed-rank, T = -7.5 - 3, N = 16, NS, minimum detectable effect of 22-228%).

Alternative Male Preferences

Rather than a preference based on novelty, males might prefer large females (e.g., high rate of egg production; Michaud 1990) or responsive females (e.g., high rate of display). We examined these alternative possibilities by determining whether male display rate, an indicator of male interest, correlated with the type of session (resident-female or novel-female), female body mass, or female display rate. However, male display rate significantly correlated only with the type of session (Stepwise regression; $F_{1,44} = 12.31$, $R = 0.47$, $P < 0.001$).

Field Experiment

All 18 focal males in the study altered their baseline behavioural profiles with the introduction of novel females (Table 3.4). A major departure from baseline was a significant decrease in the amount of time males spent on nondirected territorial activities, such as monitoring and displaying from stationary sites and patrolling. From baseline sessions to novel-female sessions, the proportion of time males spent in nondirected territorial activities decreased from 75% to less than 20% (Wilcoxon signed-rank, T = 85.5, N = 18, $P < 0.0001$), and the proportion of time spent in resident female directed activity decreased from 5.3 to 1.2% (T = 21.5, N = 18, NS, minimum detectable effect of 170%). In contrast, the proportion of time males spent directing activities towards novel females during novel-female sessions was 10-fold the proportion of time males spent directing activities toward resident females during baseline sessions (53.2 versus 5.3%, respectively; T = 83.5, N = 18, $P < 0.0001$).

During novel-female sessions, males shifted their display activity from nondirected territorial activity to novel female directed activity (Table 3.4). In baseline sessions, 94.3% of all displays occurred during nondirected territorial activity, whereas during novel-female sessions, only 44.2% of displays occurred during this context (Wilcoxon signed-rank, T = 84.5, N = 18, $P < 0.0001$). Displays directed toward resident females accounted for 5.7% of all baseline session displays and did not significantly change in proportion (4.4%) during novel-female sessions ($T = 15.5$, $N = 18$, NS, minimum detectable effect of 174%). However, 51.4% of all novel-female session displays were directed at novel females, which was significantly greater than the 4.4% of displays directed towards resident females ($T = -83.5$, $N = 18$, $P < 0.0001$). Furthermore, male display rates towards resident females decreased 10-fold from baseline to novel-female sessions (1.0 display/min versus 0.1 display/min, Table 3.4; $T = 4$, $N = 7$, NS, minimum detectable effect of 317%; 11 males that did not associate with resident females during baseline or novel-female sessions were excluded from comparisons). In contrast, during novel-female sessions male display rates toward novel females were 20-fold higher than rates toward resident females (2.0 displays/min versus 0.1 display/min; $T = 39$, $N = 12$, $P < 0.0005$; six males that did not associate with resident females during novel-female sessions were excluded from comparisons).

Four other aspects of male behaviour varied from baseline to novel-female sessions. First, very low amplitude headbob displays were directed toward novel females. Other than the low amplitude of headbob movements (about 50% of typical head amplitude), the displays resembled the typical stereotyped display cadence patterns previously reported for male *A. carolinensis* (DeCourcy & Jenssen 1994; Jenssen et al. 2000). Low-amplitude displays comprised 7.3% of displays toward novel females (novel-female sessions), but only 0.1% of displays directed toward resident females during baseline sessions (Wilcoxon signed-rank, $T = -26.5$, $N = 18$, $P < 0.0039$). Low-amplitude displays were used by nine of the18 males toward novel females, and by only two males toward resident females during baseline sessions.

Second, displays directed toward females tended to be sequenced in longer volleys during novel-female sessions than during baseline sessions (mean of 2.6 - 2.8 displays/volley during baseline sessions versus 3.4 - 4.0 displays/volley during novel-female sessions; Table 3.4), and volleys performed toward novel females were significantly longer than volleys performed during nondirected territorial activity (Wilcoxon signed-rank, $T = 56.5$, $N = 17$, $P < 0.0053$).

Third, male body colour shifted (from green to brown, or from brown to green) about twice as often during novel-female sessions as during baseline sessions (mean color change of 3.6 times/h ±2.6 versus 1.6 times/h ±2.0, respectively; Wilcoxon signed-rank, $T = -30$, $N = 18$, $P = 0.014$). The most intense male body colour shifts were associated directly with novel females. Half of the 18 males turned very dark brown (almost black) after initially sighting a novel female, and 16 males turned brown during subsequent interactions with the novel female. In comparison, only once did a male turn dark brown during interaction with a resident female.

Fourth, males were observed to use two tactics, chasing and creeping, to approach novel females. Both tactics were rare or not seen with resident females. In nine trials, the male approached a novel female by creeping slowly toward her while performing headbob displays at either a normal or low amplitude. In seven trials, the male chased the novel female, and she responded by fleeing. By chasing, three males successfully obtained a mouth hold on the female, but none were able to gain a copulatory position. Three of the seven males that initially chased a novel female later switched to a creeping approach, a tactic that was less likely to cause the female to flee. However, none of the males succeeded in copulating with a novel female within the 1-2 h novel-female sessions.

The paint marks applied to the neck and tail tips of novel females did not appear to influence male responses. There were no detectable differences in the 18 male variables examined due to the way that novel females were marked in a trial (Wilcoxon two sample tests with a continuity correction of 0.5, W ranged 7-35, NS), however, small sample sizes severely limit the ability of these tests to detect significant differences (i.e., power). Thus, we also examined the data visually for trends. If paint marks had influenced male behaviour toward novel females, the predicted trend would be a strong response toward females with the most conspicuous paint mark (e.g., on the neck, N = 5), an intermediate response toward females with an inconspicuous paint mark (e.g., tip of the tail, N = 5), and a weak response toward females with no paint mark (N = 4). Only one of the six variables that measured male responses toward novel females (Table 3.4) was consistent with the predicted trend (volley size averaged 3.72, 3.53 and 3.25 for females with painted necks, painted tails, or no paint marks, respectively), and the remaining five variables did not follow any particular trend.

Discussion

Laboratory Experiment

The laboratory experiment tested four alternative hypotheses. The first hypothesis (H_1, males do not differentially respond toward females) assumes that: males are unable to differentiate among females; males may be able to differentiate between females, but exhibit no consistent preference for particular females; or experimental conditions were not conducive to the expression of male mate choice. We dismissed all of these assumptions because male *A. carolinensis* showed consistent and significant differential responses toward the different classes of females.

The second hypothesis (H_2, males differentially respond toward females, however response is not based on a familiar/novel status) assumes that male preference is based on female traits other than relative familiarity. We examined whether male courtship responses were correlated with two female traits, body size and display rate, that could potentially increase male reproductive success. Preferentially courting and mating with larger females could enhance male reproductive success because larger females produce larger eggs (resulting in larger neonates) and lay eggs at a faster rate than smaller females (Andrews 1985; Michaud 1990). Preferentially courting and mating with females that display frequently toward a male could enhance male reproductive success if the display rate indicates a greater chance of copulating with a female (i.e., female is sexually receptive to the male), or if the display rate indicates a female's body condition (i.e., ample energy resources for vigorous display behaviour and egg production, and low likelihood of parasites or disease). We rejected all of these assumptions because male mating preferences, as indicated by male display rates, did not significantly correlate with either female body mass or female display rate.

The third hypothesis (H_3, males differentially respond toward resident and novel females, and prefer resident females) assumes there is a reproductive advantage to males who recognize, bond, and preferentially mate with a particular female, and/or there is a reproductive penalty for courting and mating with novel females. Some lizards do form exclusive pair bonds, either over short durations with different females in an expression of serial monogamy (e.g., Censky 1995; Cuadrado 1999), or long durations with the same female that reflects perennial monogamy (e.g., Bull et al. 1998). Females of these species are wide-ranging, and male reproductive success is best served by a male moving with a single mate to guard against her copulating with other males while she is sexually receptive. However, exclusive mate bonding or direct female guarding by *A. carolinensis* was not supported by either our laboratory or field experiments, nor would it be predicted from the species' polygynous mating system. In our laboratory experiment, males showed no increased interest toward re-introduced resident females that might indicate a social bond. In both our laboratory and field experiments males ignored resident females, while dramatically increasing courtship behaviour toward novel females. Furthermore, recent field studies of *A. carolinensis* describe a territory-based mating system of female-defense polygyny (Ruby 1984; Jenssen and Nunez 1998; Jenssen et al. 2001), facilitated by the distribution of females in small, stable home-ranges. Since females are not wide-ranging, males can effectively guard multiple females by defending a large territory that contains 2-6 females.

The last hypothesis (H_4, males differentially respond toward resident and novel females, and prefer novel females) was supported. In the laboratory, 14 of 16 males discriminated between a resident female and a novel female by demonstrating a consistent preference for novel females (PNF response). Compared to resident-female sessions, males during novel-female sessions significantly increased their display rate (320%), volleys of repetitive displaying (300%), volley length (150%), and significantly decreased the distance (375%) and number (430%) of movements traveled away from the female. Furthermore, our data suggest that the male PNF response was not mediated by any observable class-specific cues from resident or novel females. From the 17 variables examined, none of the measured behaviours appreciably differed between the two classes of females when introduced to individual males, nor did they appreciably differ in individual females when serving as either a resident or novel female. The only exception was related to separation distance; novel females tended to move away (i.e., retreat) from males more often than resident females, but this was due in part because males advanced toward novel females more frequently than toward resident females. In addition, there were no perceptible differences in male or female pheromone-implicated behaviours (e.g., deposition by mouth wiping and body dragging, or monitoring by tongue-touching and lip-smacking) between experimental sessions; thus, there were no indications of either deposition or detection of class-specific olfactory cues.

In summary, the laboratory results demonstrated that male *A. carolinensis* identify and preferentially court novel females over resident females (PNF response). The means by which males discriminated among females does not appear to be a simple stimulus-response mechanism based on obvious class-specific cues from females. Instead, we conclude that discrimination of females by males is best explained by individual recognition. We suggest a cognitive function, whereby males detect and remember a combination of physical and/or behavioral features unique to each resident female. Such features could include subtle variance in headbob display cadence, head and body configurations, coloration (e.g., a dorsal stripe, ultraviolet skin patterns), scars, and tail features (e.g., length, regrowth, or kinks). Males then identify a female as "novel" because she does not match any remembered combinations of resident-unique features.

Field Experiment

The results of the field experiment both validated the conclusions of our laboratory experiment, and provided additional quantitative and qualitative information on male responses under natural conditions. In all 18 of the naturally occurring, polygynous breeding groups used in our field test, free-ranging *A. carolinensis* males showed an immediate and intense response to introduced novel females that contrasted dramatically with the interactions of the same males toward resident females.

The most compelling evidence for a PNF response in free-ranging *A. carolinensis* is the way that males reapportioned the amount of time spent in typical social activities (e.g., monitoring, advertisement displaying, territorial patrol, boundary defense, and courtship; Jenssen et al. 1995). After novel females were sighted, males decreased the proportion of time and displays devoted to non-directed, territorial activities (e.g., patrol, advertisement), and decreased the proportion of time and displays devoted to resident female interactions. Rather, males allocated the greatest proportion of their time and displays to the pursuit of novel females (Table 3.4). The magnitude of re-directed social activities indicate the extent to which males reapportion their attention and priorities toward novel females.

In addition to shifts in male activity profiles, novel females in the field experiment also appeared to elicit three qualitative male responses rarely or never observed toward free-ranging resident females, nor in our laboratory interactions. These three responses may indicate that encounters with novel females elicit high levels of male arousal. The first response was a rapid shift of body colour from green to very dark brown, an indication that melanophores were responding to the release of epinephrine and nor-epinephrine (Cooper & Greenberg 1992). In general, shifts in male body colour were twice as frequent during novel female introductions as during baseline observations. The second response was the use of chase and/or creep tactics by free-ranging males to approach novel females. Chasing, the expected response of a highly motivated male, caused females to flee from rapidly advancing males, and three males subsequently switched to a creep approach that allowed them to get closer to novel females. Eleven males exclusively used the creep tactic, perhaps due to prior social experience that influenced their choice of a less expeditious, but more effective approach tactic. The third response consisted of very low-amplitude headbob displays directed to novel females. The amplitude of headbob displays is typically related to effective signaling distance; low amplitude displays would have a shorter transmission or detection distance (Fleishman 1992; Orrell & Jenssen 1998). However, males in the laboratory and free-ranging males courting resident females did not use low-amplitude displays, even when lizards were only a few centimeters apart. Thus, separation distance is not an explanation for diminished head amplitude during signaling. We speculate that the low-amplitude displays emanate from a conflicted arousal state, where a male is highly motivated to convey sexual interest to a novel female by displaying, while this same behaviour could cause an uncertain and non-resident female to flee.

In summarizing the field experiment, we make three points. First, the shift in social activity profile of males, the elevated arousal levels males exhibited after sighting a novel female, the high display rates males used to court novel females, and the different approach tactics males used in the pursuit of novel females, provide support for a PNF response in free-ranging males. Second, in reapportioning their attention and priorities, male *A. carolinensis* exhibited flexible, condition-dependent patterns of behaviour that required cognitive discrimination among individual conspecifics to identify new mating opportunities. Third, the extent to which males altered their behaviour when novel females were present can be taken as a quantitative measure of selection pressure for the PNF response. Unlike laboratory subjects within unnatural confinement and prescribed social contexts, free-ranging lizards reflect the full expression of voluntary behaviours under field conditions.

Cognitive perspective

If cognition is defined as the acquisition, processing, storage, and use of information from the environment to match contingent events with appropriate behaviour (Shettleworth 1999, 2001), then our observations lend support that the PNF response is a cognitive process in *A. carolinensis*. Many studies of communication, partner choice, food caching and recovery, and navigation and orientation deal with cognitive abilities in their subjects (e.g., Balda et al. 1998; Dukas 1998). We suggest that the reproductive behaviour of male *A. carolinensis* also appears to be a potential model of cognition. The PNF response, which our data suggest is based on individual recognition (i.e., a cognitive ability), is one aspect of a mating system in which males appear to manage a host of reproductive events within their territories. Consider that a polygynous male averages three (2 - 6) resident females in his territory, each of whom cycles a single-egg clutch at weekly intervals throughout a 4-month breeding season. Thus, a male has a long-term association with a number of females, with his reproductive success dependent on multiple ovulatory events scattered through time. Therefore, selection should favor males who can distinguish among familiar resident females, recognize a novel female by default, and at some level track his mating history with each female.

Besides the present study, other field observations of *A. carolinensis* (Jenssen et al. 1995; Jenssen & Nunez 1998) offer three lines of evidence for the cognitive ability of males to remember individual resident females, track a mating history with them, and then presumably use this information to optimize mating decisions. First, males displayed at significantly different rates when approaching receptive versus non-receptive resident females, implying an ability to discriminate sexual receptivity of resident females. Second, males bypassed approximately 70% of mating opportunities with receptive resident females, implying male-determined priorities for copulation with individual females. Third, males copulated only when courtship was male-initiated, never when females initiated courtship, implying a pre-existing male intent. Although they frequently encountered resident females, males copulated only about once/day; yet eventually mated with each resident female within every observed receptive period. The advantages to males who track their mating history with resident females would include less time and energy expended in excessive bouts of courtship and copulation, more time and energy available for territorial activity (an important 75% of daily activity, Jenssen et al. 1995; present study), and less sperm depleted to unnecessary copulations with previously inseminated females. The present study adds to this list the advantage of recognizing a new mating opportunity and giving it top priority.

Cognitive mechanisms may be widely represented in lizards. There is evidence that a number of species can differentiate among individual conspecifics, and use this ability to make adaptive decisions about the course of behaviour they follow. The PNF response has been reported in two other species of territorial, polygynous lizards (*Holbrookia propinqua*, Cooper 1985; *Anolis sagrei*, Tokarz 1992). Two skink species were reported to tongue-flick more frequently toward chemical stimuli of novel females than that of familar females (*Eumeces laticeps*, Cooper 1996; *Eublepharis macularius*, Steele and Cooper 1997). Familiar mate recognition and mate scent trailing have been reported for two monogamous skinks (e.g., *Tiliqua rugosa*, Bull et al. 1998; *Niveoscincus microlepidotus*, Olsson and Shine 1998), where males form long-term pair bonds with single females, presumably as a form of mate guarding. Neighbor recognition (i.e., dear enemy phenomenon, *sensu* Temeles 1994) has been reported in *A. carolinensis* (Quails and Jaeger 1991), *Dipsosaurus dorsalis*, (Glinski & Krekorian 1985), *Crotaphytus collaris* (Fox & Baird 1992), *Lacerta agilis* (Olsson 1994), and *Platysaurus broadleyi* (Whiting 1999).

In summary, we documented a PNF response for males of *A. carolinensis*, a response that appears to be strongly selected. Our data infer that PNF is based on the cognitive ability of males to individually recognize familiar females, and differentiate them from novel females. From additional observations by other field studies, it seems that the PNF response is a subset of a more inclusive cognitive process, with which *A. carolinensis* males make mating decisions based on specific information about individual females. We suggest that *A. carolinensis* males are controlling when and with which females they will court and mate according to male-oriented contingencies. One such contingency is that novel females take mating precedence over resident females.

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Table 3.1. List of 22 variables examined to evaluate the preference for novel female (PNF) response in male *Anolis carolinensis* during laboratory and field experiments (M, F indicates variables examined for both sexes and M indicates variables examined only for males)

Lab	Field	Variable (description)
M, F	–	Subject size (Snout-vent-length, mass)
M, F	M	Number of headbob displays performed
M, F	M	Proportion of headbob displays accompanied by dewlap extension
M, F	M	Number of dewlap extensions performed without a headbob display
M	M	Proportion of headbob displays accompanied by shudderbobs (not used by females)
M, F	M	Proportion of headbob displays accompanied by display modifiers (e.g., crests, lateral compressions, gular)
–	M	Proportion of low amplitude headbob displays (amplitude about 50% of typical headbob displays)
M, F	M	Proportion of headbob displays performed singly or in a volley of 2 or more displays sequenced < 2 s apart
M, F	M	Volley size (e.g., volley of 5 successive headbob displays)
M, F	M	Position of a headbob display in a volley (e.g., 1st of 5 successive displays)
M, F	M	Distance (cm) traveled and whether travel was toward or away from another lizard
M, F	M	Number of moves made and whether moves were toward or away from another lizard
M, F	M, F	Estimated separation distance (cm) between subjects during headbob displays or interactions
M, F	–	Number of headbob display bouts initiated by the male (or female)
M, F	M, F	Number of copulations and attempted or successful forced copulations
M, F	M, F	Number of chases (e.g., male chases female, or resident female chases novel female in field study)
M, F	M	Number of creeps (very slow movements)
M, F	–	Number of lip smacks (mouth is opened and closed)
M, F	M	Number of substrate licks (tongue is touched to a surface)
M, F	M	Number of mouthwipes (side of mouth is wiped on a surface)
M, F	M, F	Body colour (green, green-brown, brown, dark-brown) and number of colour changes

Table 3.2. Descriptive statistics [mean ±SD (range)] for 17 variables recorded for female *Anolis carolinensis* during three types of laboratory sessions (baseline, resident-female, and novel-female), and Wilcoxon signed-rank (*N* = 16) statistics for comparison of variables during resident vs. novel-female sessions. Asterisks indicate the magnitude of statistically detectable difference (***< 100%, **100-200%, * >200%) between baseline and resident-female sessions (baseline column of data), and between resident-female and novel-female sessions (novel-female column of data) at a power level of 90%. [Note: none of the P-values were statistically significant following sequential Bonferroni adjustments (Rice 1989)].

Female	Laboratory Session			Wilcoxon	
Behaviours	Baseline	Resident-female	Novel-female	T	P
Displays/h	19.4 ±11.0 (2-46)***	24.0 ±15.9 (0-55)	20.3 ±16.5 (3-48)***	9.5	0.64
Dewlaps/h[1]	0.5 ±0.9 (0-3)*	0.1 ±0.2 (0-1)	0.7 ±1.4 (0-5)*	-1.5	0.50
Displays w/no response	10.4 ±10.3 (0-31)**	8.4 ±9.8 (0-35)	5.9 ±12.3 (0-41)**	26	0.15
% Displays w/dewlap	2.4 ±7.6 (0-30)***	0.1 ±0.5 (0-2)	7.3 ±14.7 (0-50)	9.5	0.06
Volleys/h	3.2 ±2.6 (1-8)**	4.8 ±3.3 (1-8)	4.0 ±1.4 (3-5)*	2.5	0.63
Volley size[2]	2.2 ±0.4 (2-4)***	2.5 ±0.5 (2-4)	2.2 ±0.2 (2-3)**	3	0.38
Colour changes/h	0.1 ±0.2 (0-1)***	0.1 ±0.3 (0-1)	0.2 ±0.4 (0-1)*	-1	1.0
Lip smacks/h	12.1 ±24.0 (0-102)*	4.3 ±5.0 (0-18)	7.1 ±8.8 (0-32)*	-14.5	0.47
Substrate licks/h	3.9 ±3.4 (0-13)**	4.0 ±5.4 (0-23)	4.7 ±2.6 (0-9)**	-26.5	0.14
Mouthwipes/h	1.9 ±1.8 (0-6)*	1.3 ±2.4 (0-10)	0.4 ±0.6 (0-2)**	12	0.13
Body drags/h	0*	0.8 ±1.8 (0-7)	0.4 ±1.2 (0-5)*	4	0.56
% Distance toward[4]	32.3 ±24.7 (0-100)**	29.8 ±17.7 (0-61)	16.1 ±14.0 (0-40)***	40.5	0.019
% Moves toward[5]	29.5 ±24.5 (0-100)**	23.3 ±12.4 (0-44)	16.6 ±15.0 (0-43)***	25	0.16
% Distance away[6]	24.1 ±20.3 (0-57)***	31.1 ±15.8 (9-67)	51.2 ±30.4 (0-100)***	-44	0.021
% Moves away[7]	23.3 ±19.5 (0-60)***	31.4 ±18.1 (7-67)	46.6 ±29.9 (0-100)***	-38	0.049
Total moved m/h	2.2 ±1.6 (0.4-5.3)***	2.1 ±1.2 (0.6-5.0)	2.8 ±2.3 (0.8-1.0)**	-11.5	0.57
Total #moves/h	15.1 ±12.0 (1-52)***	15.1 ±8.1 (6-35)	15.4 ±8.7 (5-35)***	-1.5	0.95

[1] Dewlap extensions or pulses given without a headbob display.

[2] Comparisons performed using mean volley size for each subject and session.

[3] Total static modifiers, including: crests, lateral compressions, and gular expansions.

[4] The percentage of the total distance moved which was toward the other lizard.

[5] The percentage of the total number of moves which were toward the other lizard.

[6] The percentage of the total distance moved which was away from the other lizard.

[7] The percentage of the total number of moves which were away from the other lizard.

Table 3.3. Descriptive statistics [mean ±SD (range)] for 22 variables recorded for male *Anolis carolinensis* during three types of laboratory sessions (baseline, resident-female, and novel-female), and Wilcoxon signed-rank (*N* = 16) statistics for comparison of variables during resident vs. novel-female sessions. Asterisks indicate the magnitude of statistically detectable difference (***< 100%, **100-200%, * >200%) between baseline and resident-female sessions (baseline column of data), and between resident-female and novel-female sessions (novel-female column of data) at a power level of 90%. [Note: only P-values in boldface were statistically significant following sequential Bonferroni adjustments (Rice 1989)].

Male	Laboratory Session			Wilcoxon	
Behaviours	Baseline	Resident-female	Novel-female	T	P
Displays/h	18.4 ±15.6 (0-51)***	20.0 ±12.6 (0-40)	64.3 ±53.8 (1-176)*	-57	**0.0016**
Dewlaps/h[1]	0.3 ±0.7 (0-2)**	0.3 ±0.7 (0-2)	0.3 ±0.6 (0-2)*	-0.5	1.0
Displays w/no response	5.9 ±8.1 (0-32)**	5.9 ±8.7 (0-25)	33.4 ±36.2 (0-122)*	-30	0.005
% Displays w/dewlap	99.3 ±1.4 (96-100)***	98.4 ±3.4 (88-100)	98.2 ±3.8 (89-100)***	-1	0.95
% Displays w/shudderbob	17.8 ±26.5 (0-100)***	27.8 ±29.5 (0-100)	33.7 ±37.8 (0-100)**	-6.5	0.67
Volleys/h	5.6 ±4.4 (1-17)***	6.0 ±2.7 (1-11)	17.9 ±11.0 (1-36)**	-36	**0.0024**
Volley size[2]	2.4 ±0.4 (2-5)***	2.5 ±0.4 (2-5)	3.7 ±1.0 (2-17)***	-33	**0.001**
Crests/h	0.1 ±0.5 (0-2)*	0	0.6 ±1.1 (0-3)*	-5	0.13
Lateral compressions/h	0	0	1.5 ±3.1 (0-12)*	-7.5	0.06
Gular expansions/h	0.1 ±0.2 (0-1)*	0.1 ±0.2 (0-1)	0.8 ±1.9 (0-8)*	-5	0.13
All static modifiers/h[3]	0.2 ±0.7 (0-3)*	0.1 ±0.2 (0-1)	2.9 ±5.7 (0-23)*	-14	0.016
Colour changes/h	0.4 ±0.7 (0-2)**	0.4 ±0.7 (0-2)	0.6 ±1.1 (0-4)*	-4	0.75
Lip smacks/h	3.8 ±5.8 (0-20)**	2.9 ±3.5 (0-14)	3.9 ±5.0 (0-17)**	-7.5	0.69
Substrate licks/h	1.9 ±1.9 (0-6)**	2.2 ±2.4 (0-8)	2.9 ±3.3 (0-10)**	1	1.0
Mouthwipes/h	1.3 ±1.6 (0-3)**	0.6 ±1.3 (0-5)	0.3 ±0.8 (0-3)*	3	0.69
Body drags/h	0***	0.2 ±0.5 (0-2)	0.2 ±0.4 (0-1)*	0	1.0
% Distance toward[4]	27.6 ±20.0 (0-70)***	30.0 ±20.2 (0-79)	58.0 ±29.9 (0-100)**	-47	0.013
% Moves toward[5]	25.6 ±16.3 (0-54)***	26.3 ±15.8 (0-45)	55.6 ±29.1 (0-100)**	-51	0.006
% Distance away[6]	35.4 ±25.7 (0-94)***	38.3 ±23.7 (0-100)	10.2 ±16.2 (0-63)***	51.5	**0.002**
% Moves away[7]	37.8 ±26.8 (0-93)***	34.9 ±21.6 (0-100)	8.1 ±8.9 (0-29)***	60	**0.0007**
Total moved m/h	3.3 ±2.2 (0.4-8.2)***	3.7 ±4.1 (0.1-1.6)	1.9 ±1.6 (0.2-7.2)***	33	0.09
Total #moves/h	16.1 ±10.4 (1-44)**	26.6 ±41.8 (1-182)	22.5 ±47.2 (2-204)***	19.5	0.33

[1] Dewlap extensions or pulses given without a headbob display.

[2] Comparisons performed using mean volley size for each subject and session.

[3] Total static modifiers, including: crests, lateral compressions, and gular expansions.

[4] The percentage of the total distance moved which was toward the other lizard.

[5] The percentage of the total number of moves which were toward the other lizard.

[6] The percentage of the total distance moved which was away from the other lizard.

[7] The percentage of the total number of moves which were away from the other lizard.

Table 3.4. Descriptive statistics [mean ±SD (range)] for six variables recorded for 18 free-ranging male *Anolis carolinensis* during baseline and novel female sessions and three types of social contexts.

	Social context		
	Nondirected[1]	Resident-female	Novel-female
Baseline session:			
% time/session[2]	75.0 ±20.9 (37-100)	5.3 ±10.2 (0-33)	-
% displays/session[3]	94.3 ±6.4 (79-100)	5.7 ±6.4 (0-21)	-
Displays/min[4]	2.2 ±0.7 (1-4)	1.0 ±1.6 (0-5)	-
% low-amp displays[5]	0.8 ±1.3 (0-4)	0.1 ±0.3 (0-1)	-
% displays in volleys[6]	60.1 ±9.7 (47-85)	69.1 ±37.5 (0-100)	-
Volley size	2.6 ±0.3 (2-8)	2.8 ±0.6 (2-6)	-
Novel female session:			
% time/session[2]	18.8 ±19.1 (0-65)	1.2 ±2.1 (0-9)	53.2 ±24.3 (3-100)
% displays/session[3]	44.2 ±27.5 (0-86)	4.4 ±10.7 (0-46)	51.4 ±27.1 (9-100)
Displays/min[4]	2.9 ±1.6 (0-8)	0.1 ±0.3 (0-1)	2.0 ±1.1 (0-5)
% low-amp displays[5]	0.5 ±1.4 (0-6)	0	7.3 ±14.3 (0-61)
% displays in volleys[6]	58.2 ±22.7 (0-100)	82.3 ±35.5 (0-100)	70.9 ±21.8 (0-100)
Volley size	2.6 ±0.5 (2-6)	4.0 ±1.4 (2-6)	3.4 ±0.9 (2-23)

[1] Nondirected context refers to territorial activities (territorial advertisement, patrol, and monitoring).
[2] Proportion of each session that males spent in nondirected, resident-female, and novel-female social contexts (not shown is time spent in nonterritorial and nonsocial activities such as feeding).
[3] Proportion of all displays in a session performed during nondirected, resident-female, and novel-female social contexts.
[4] Rate of displays/min discounting periods of time that males were not displaying.
[5] Proportion of displays performed as low-amplitude variants.
[6] Proportion of volleyed displays (2 or more sequential displays <2 s apart).

CHAPTER 4

Comparison of energy expenditure by male and female *Anolis carolinensis* during breeding and postbreeding seasons

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Abstract

Although the amount of energy that males and females expend for reproduction is an integral component of theories explaining the evolution of particular mating strategies, few studies have actually determined the energy each sex allocates to reproduction. We examined energy expenditure of male and female *Anolis carolinensis* lizards during breeding and postbreeding seasons. Laboratory respirometry was used to determine resting metabolic rates (RMRs) of inactive, freshly captured lizards, and the doubly-labeled water technique was used to determine field metabolic rates (FMRs) of free-ranging lizards. Both RMRs and FMRs were significantly influenced by body mass. Sex did not influence RMRs. However, RMRs of both sexes significantly increased from breeding to postbreeding season (~ 40%). We attribute the seasonal increase in RMRs to a post-reproductive increase in feeding rate and the effect of specific dynamic action. Neither sex nor season significantly influenced FMRs.

The RMRs and FMRs were used in combination with lizard thermal profiles to calculate energy budgets for males and females during breeding and postbreeding seasons. Energy budgets partitioned daily field energy (DFE; calculated from FMRs) into daily activity energy (DAE) and daily resting energy (DRE; calculated from RMRs). The energy expended for reproduction was estimated for males as DAE during the breeding season, and for females as DAE during the breeding season plus egg production. Despite males having 40% greater body mass, females expended 46% more energy for reproduction than males (906 J/day and 619 J/day, respectively). Total maintenance energy (TME = DFE + egg production for females) expended during the breeding season was similar for both sexes (1280 and 1365 J/day, respectively). Although TME of females decreased from breeding to postbreeding season (1365 versus 766 J/day, respectively), TME of males was similar during both seasons (1280 versus 1245 J/day, respectively). There were both seasonal and sexual differences in DRE and DAE. In comparison to other species of lizards, *A. carolinensis* in a temperate habitat expend more total energy during the breeding season, allocate more energy to eggs, and appear to have more total energy available for reproduction, than most lizards from semiarid/desert habitats.

Introduction

As early as 1871, Darwin recognized that there were fundamental differences in the ways that males and females allocate energy to reproduction. He pointed out that, "on the whole, the expenditure of matter and force by the two sexes is probably nearly equal, though effected in very different ways and at different rates." Subsequently, differential investment by each sex in gametes (i.e., anisogamy; Bateman 1948) and individual offspring (Trivers 1972) became central concepts in the development of theories explaining the evolution of male and female mating strategies (e.g., Williams 1966a,b; Orians 1969; Arnold and Duvall 1994). In general, reproductive investment by females consists of resources allocated directly to the production of relatively few, but energetically expensive, gametes. In some species, females also make a substantial investment in the care of neonates. Thus, the reproductive output of females is believed to be primarily resource limited (Bateman 1948; Trivers 1972). Females may optimize reproductive success by allocating more energy (and/or parental care) to individual offspring to produce a few large or higher quality neonates, or by allocating less energy to individual offspring to produce a greater number of small neonates (Trivers 1972; Smith and Fretwell 1974).

In contrast to females, the energy that males invest in the production of gametes is typically minimal. Thus, the reproductive success of males is not usually limited by the amount of energy available for gamete production, but by the ability to compete for and successfully mate with females (Bateman 1948). As a result, males may invest a great deal of energy for activities and traits associated with male reproductive success (e.g., advertisement displays, territorial defense, agonistic encounters, courtship, large body size, structures used for courtship or inter-male combat; Bateman 1948; Trivers 1972). In addition, the time-intensive reproductive activities of males may limit the time spent in energy acquisition (Congdon 1989). For males that invest minimal energy directly in gametes, they can optimize reproductive success by allocating energy to activities and/or structures that maximize the number of offspring sired (e.g., that increase mating opportunities, mating success, and protection of paternity).

Together, Bateman’s concept of anisogamy (1948) and Triver’s concept of parental investment (1972), suggest how the energy allocated by each sex to reproduction relates to the evolution of particular mating systems. For instance, when males contribute paternal care to offspring and/or provide nuptial benefits to females, care-providing males do not have the energy or time to pursue multiple mates, and a monogamous mating system usually results. When monogamous males and females expend about the same amount of energy for parental care and produce about the same number of offspring, then both sexes should also allocate a similar amount of energy to individual offspring. In contrast, males emancipated from parental care typically invest time and/or energy resources to defend or pursue multiple mates, contributing to a polygynous mating system and intense inter-male competition for mates. Because polygynous males typically allocate a great deal of energy to structures and/or behaviors that benefit their mating success, males may still invest as much energy in reproduction as females. However, since polygynous males typically produce a greater number of offspring than females (Bateman 1948; Trivers 1972), the amount of energy that males allocate to individual offspring should be less than that allocated by females.

Despite the important role that reproductive energetics may have in helping to understand the evolution of mating systems and reproductive behaviors, comparisons of the relative amount of energy that males and females allocate to reproduction are few (Bennett and Nagy 1977; Congdon 1977). Although several studies have examined ‘costs’ associated with reproduction, most research has focused on costs in terms of reduced mobility and fecundity, or increased predation or mortality, rather than direct physiological or energetic costs (studies reviewed by Schwartzkopf 1994). The lack of studies on reproductive energetics may, in part, be due to the difficulty in measuring the energy expended for reproductive activity (e.g., behaviors related to territory, resource or mate defense, and courtship). Although measurement of female reproductive allocation to eggs became relatively easy and inexpensive with the development of bomb calorimetry techniques over 40 years ago (Golley 1961; Phillipson 1964), measuring the energy allocated to reproductive activity by free-ranging animals relies on the doubly-labeled water technique (using oxygen-18 and deuterium or tritium isotopes; Lifson and McClintock 1966; Nagy 1983a), which remains a relatively difficult and expensive procedure.

We chose the green anole, *Anolis carolinensis*, as a model organism for examining the relative energy that males and females allocate to reproduction for several reasons: 1) territorial *A. carolinensis* lizards have high site fidelity (Ruby 1984; Jenssen et al. 1995a) and provide a high probability for recapture after being captured and released; 2) neither sex uses fat stores accumulated prior to the breeding season for reproduction (Wade 1981; Michaud 1990) or provides post-hatch parental care, simplifying the task of determining the energy expended for reproduction; and 3) the life history traits and mating system of *A. carolinensis* are well documented and provide a basis for relating the energy expended by each sex to their respective reproductive strategies (Ruby 1984; Jenssen et al. 1995a; Jenssen and Nunez 1998; Jenssen et al. 2001).

The female-defense polygyny of *A. carolinensis* is largely an outcome of the distribution of reproductive females in space and time, and the response of males to this distribution (e.g., Partridge and Endler 1987; Davies 1991; Sutherland 1996). Females lay single-egg clutches at about weekly intervals (Andrews 1985; Michaud 1990) throughout a four-month breeding season (Jenssen et al. 1995a). Distributed in stable, small (~ 8 m^3), overlapping (~ 20%), and lightly defended (~ one aggressive encounter/day) home ranges, females are relatively sedentary, performing less than 14 displays/h and traveling less than four m/h (Nunez et al. 1997; Jenssen and Nunez 1998). Small female home ranges and infrequent competitive interactions between neighboring females suggest that the resources needed for egg production are not critically limited (Jenssen and Nunez 1998).

In response to clumped, sedentary, and iteroparous females, *A. carolinensis* males attempt to monopolize multiple females by means of territorial defense (Ruby 1984; Jenssen et al. 1995a; Jenssen and Nunez 1998). Inter-male contests for habitat containing females result in a 1:3 male-to-female breeding ratio in populations with 1:1 adult sex ratios (Ruby 1984; Jenssen et al. 1995a). As a consequence of female-defense polygyny, the potential reproductive rate among territorial males is positively correlated with male body size, size of male territory, number of defended (i.e., resident) females, and the duration of time a male defends his territory (Ruby 1984; Jenssen and Nunez 1998). Intrasexual selection on males may contribute to prominent sexual dimorphisms. In comparison to females, males are 30-40% larger in body mass (Jenssen et al. 1995b; current study), have eight-fold greater territory volume (69 m^3 versus 8 m^3), move six-fold greater distances per unit of time (27 m/h versus 4 m/h), display seven-fold more frequently (100 displays/h versus 14 displays/h), and spend a 30-fold greater proportion of the day in consexual dispute (9.2% versus 0.03%) (Jenssen et al. 1995a; Jenssen and Nunez 1998; Nunez et al. 1997). That territorial males lose body mass and have an apparent 75% attrition rate by the end of the 4-month breeding season (Ruby 1984) suggests that males expend a great deal of energy on reproductive activity.

The sexually divergent reproductive strategies and behaviors associated with a polygynous mating system suggest the following testable hypotheses regarding the energy that male and female *A. carolinensis* expend for reproduction:

H_1: Males and females allocate about an equal amount of energy to reproduction for an entire breeding season.

H_2: During the breeding season, males allocate more energy to activity than females, due to the dramatic difference in activity between territorial males and sedentary females.

H_3: The rate of total energy (total maintenance energy) expended by both sexes are greater during the breeding season than during the post-breeding season, due to the energy that males expend for territorial activity and that females expend for egg production during the breeding season.

To test our hypotheses, we used an energy budget (Fig. 4.1) to partition daily energy allocation to resting and activity energy (Congdon et al. 1982). Thermal profiles of field subjects were used in combination with resting metabolic rates (RMRs in ml O_2/h, determined by laboratory respirometry) to estimate the daily resting energy (DRE) expended. The doubly-labeled water technique (Nagy 1983a) was used to determine field metabolic rates (FMRs in ml CO_2/day) of free-ranging lizards, then FMRs were converted to energy equivalents to represent the daily field energy expended (DFE in Joules/day). Daily activity energy (DAE) was then calculated as the difference between DFE and DRE (DAE = DFE - DRE). The total energy expended for reproduction was estimated as the energy that males allocate to activity during the breeding season, and energy that females allocate to activity and egg production during the breeding season. Although males also allocate energy to reproduction in the production of sperm and ejaculate, the amount of this energy cannot be determined and is assumed to be minimal. The total maintenance expenditure (TME) was calculated as the DFE plus the energy allocated to production (e.g., growth, storage, egg production).

Our goals for this study were to: 1) measure and compare rates of resting metabolism and daily field energy to determine the influence that sex and season have on metabolism (independent of intersexual differences in body size); 2) use energy budgets to test the working hypotheses above; 3) relate energy expenditure to the particular mating strategy and life history traits of *A. carolinensis*; and 4) compare the energy expended for reproduction by *A. carolinensis* to that previously published for other lizard species.

Methods

Thermal profiles.

An average 24 h thermal profile for lizards at the Augusta Canal study site was compiled from measured ambient temperatures (T_A), measured lizard body temperatures (T_B), and lizard activity profiles (Jenssen et al. 1995a; Nunez et al. 1997) as follows. For 10 days during the breeding season and 19 days during the post-breeding season (while the study was in progress), ambient air temperatures were recorded hourly on the study site at sunny and shaded locations using Hobo data-loggers® (Fig. 4.2). To prevent direct solar heat absorption, the data-logger temperature probes were suspended in 8-ounce metal cans that were open at both ends, and had the surfaces covered in white, reflective tape. Because the average air temperatures did not appreciably change from breeding to postbreeding season (Fig. 4.2), we used the same thermal profile to calculate energy budgets for both seasons. For the 8 h photophase when lizards were maintaining T_B by thermoregulation (0900-1700 h), we measured the mean (± SD) cloacal temperatures of active lizards as being 33.4°C ± 1.0 ($n = 16$). During the 11 h scotophase (2000 - 0700 h), the average T_B of lizards was estimated to be the same as average night-time T_A (23°C; Fig. 4.2). For the first and last hour of the photophase (0700 - 0800 and 1900 - 2000 h) when lizards could not thermoregulate, average T_B was also estimated to be the same as average T_A (e.g., 23°C). During the 3 h of photophase (0800 - 0900 and 1700 - 1900; Fig. 4.2) when the sun was low on the horizon and tall trees blocked most direct sunlight, we assumed that the transition between 23°C and 33°C resulted in an average T_B of 28°C.

Resting metabolic rates

To mimic the condition of free-ranging lizards that are usually digesting prey, we determined resting metabolic rates (RMRs in volume O_2 consumed/h) within 24 h of capturing lizards, while digestion of previously captured prey was presumably still in progress (Windell and Sarokon 1976). The RMRs of recently captured lizards should reflect the metabolic cost of digestion (e.g., specific dynamic action or SDA; Niewiarowski and Waldschmidt 1992), but not the potential effects that long-term laboratory acclimation could have on metabolism (Beyer and Spotila 1994). The RMRs of freshly captured lizards should more accurately represent the resting metabolism of free-ranging lizards than standard metabolic rates of fasted, laboratory-acclimated lizards. In addition, since RMRs often exhibit diel variation (Niewiarowski and Waldschmidt 1992; Beaupre et al. 1993), RMRs were measured every 40 min during the scotophase (2000 - 0700 h) and then averaged for each lizard. Different lizards were used to determine RMRs for each temperature and season.

Lizards were allowed 2 h of acclimation in clear glass containers (150 - 360 ml) within a dark chamber, then rates of O_2 consumption were measured at 40 min intervals with a Micro-Oxymax® system (Columbus Instruments, Columbus, OH). The Oxymax® is a closed system with a reference chamber that recalibrates the sensors after each measurement and normalizes rates of O_2 consumption for standard temperature (0ºC) and pressure (760 mm Hg; Columbus Instruments 1993). Air in the chambers was refreshed after each measurement to maintain constant O_2 and CO_2 concentrations.

We determined RMRs at 28ºC (*n* = 17) and 33ºC (*n* = 7) during the breeding season (July), and at 28ºC (*n* = 31) during the postbreeding season (August). We did not determine RMRs at 33ºC during the postbreeding season because some lizards at this temperature during the breeding season exhibited signs of stress (mouth-gaping), and one lizard died following the measurements.

Additional RMRs required to partition the energy budget, at 23ºC during the breeding season, and at 23ºC and 33ºC during the postbreeding season, were estimated as follows (also described in Appendix 4.1). First, we calculated Q10 values based on known temperature-specific metabolic rates. Although the term Q10 refers to the increase in metabolic rate associated with a 10ºC increase in temperature, a Q10 may be calculated for any temperature interval (Schmidt-Nielsen 1990). We calculated Q10 values for: 1) the temperature interval of 28 - 33ºC using the measured scotophase RMRs for the breeding season; and 2) the temperature interval of 23 - 28ºC using standard metabolic rates determined on fasted, winter *A. carolinensis* by Jenssen et al. (1996). Q10 values were calculated using the equation: $Q10 = (RMR2/RMR1)^{10/T2-T1}$ where RMR1 and RMR2 are the RMRs for temperatures T1 and T2, respectively. Second, estimated RMRs were based on the appropriate Q10 values and temperature and season-specific RMRs using the following equation: $RMR1 = RMR2/(Q10)^{1/2}$, where RMR1 is the estimated RMR for temperature T1, RMR2 is the known RMR for temperature T2, and the Q10 value is for the temperature interval T1-T2. Third, since RMRs were measured on sleeping lizards (scotophase), RMRs were multiplied by 1.4 to obtain respective photophase RMRs for alert lizards during the day (based on scotophase and photophase metabolic rates reported for other lizards; Andrews and Pough 1985; Beaupre et al. 1993; van Marken Lichtenbelt et al. 1993) (see Appendix 4.1 for more details).

Field metabolic rates

We used the doubly-labeled water method (Nagy 1983a) to determine water influx rates (WIRs;

ml H_2O/day) and field metabolic rates (FMRs; volume CO_2 expired/day) in free-ranging *A. carolinensis* during breeding and postbreeding seasons. The WIRs were used to estimate the amount of free water intake. During the breeding season (June-July), subjects were established territorial males and gravid females (i.e., an egg could be palpated). During the postbreeding season (mid-August) male subjects were individuals previously identified as territorial residents during the breeding season.

Lizards (54 males, 43 females) were weighed (± 0.1 g), measured for SVL, toe-clipped for identification, and given an intra-peritoneal injection of an isotope mixture (3.75 ml of deionized, distilled water, 1.25 ml of 95 atom% H_2O^{18}, and 0.34 ml of 99.7 atom% D_2O) at a volume of 7.5 µl/g body mass. At least 2 h were allowed for the isotopes to equilibrate with the body-water pool. Then, a 60 - 80 µl sample of blood was obtained from each lizard through a 2 - 3 mm incision in the postorbital capillary bed. Incisions healed within a few days and did not appear to impair the function of the eye or eyelid. Blood was collected in heparinized, hematocrit, capillary tubes that were capped in the field with critocaps and flame-sealed at the end of the day. Samples were kept on ice while in the field and thereafter refrigerated at 3 - 4°C until analysis. After initial samples were taken, most lizards were released at their original capture site. In a few cases where high trees or dense vegetation would have made it difficult to recapture some females, they were released into habitats that contained climbable trees and/or moderate undergrowth. Based on recapture locations, females tended to remain in the general area in which they were released.

Forty-eight lizards were recaptured 4 - 12 days after their release (mean = 8.0 ± 1.9 SD), at which time we obtained a second 60 - 80 µl sample of blood from each and redetermined their body mass. We also obtained 60 - 80 µl samples of urine (at isotopic equilibrium with blood; Nagy and Costa 1980) from four lizards that yielded inadequate blood (< 40 µl) for the second sample. Blood samples were also obtained from four unlabeled lizards (two territorial males, two reproductive females) for determination of isotope background levels. The average (± SD) background concentration of O-18 was 0.01576 ± 0.00015 atom% , and of D_2O was 0.200587 ± 0.000519 atom%.

Blood and urine samples were distilled under vacuum to obtain pure water, then isotope concentrations were determined by isotope-ratio mass spectroscopy at the Stable Isotope Lab of Boston University. At least two independent replicates (mean = 2.4 ± 0.7 SD) were analyzed for each sample and average isotope concentrations were used in calculations. We used data from 36 of the 48 recaptured lizards to calculate WIRs and FMRs. The remaining 12 recaptured lizards did not provide usable isotope data because of insufficient sample volume, capillary tube leakage, or isotope concentrations that were too close to background levels (due to isotope leakage from the injection site, or to complete turnover of isotopes). The maximum sample interval before there was a complete turnover of isotopes was about 12-13 days, with mean (± SD) initial isotope concentrations of 0.3757 ± 0.0299 atom% O-18 and 0.0631 ± 0.0074 atom% D_2O.

We calculated WIRs and FMRs according to the equations of Lifson and McClintock (1966) as modified by Nagy (1980). Total body water content was determined by drying the bodies of three postbreeding females and five postbreeding males in an oven at 65ºC to a constant body mass. Mean (± SD) body water content of live body mass was 72.4% ± 0.01 for females, 70.0% ± 0.02 for males, and 70.9 % ± 0.02 for both sexes. Rates of FMR in ml CO_2/day were converted to energy equivalents (termed daily field energy or DFE) using the value 25.7 J/ml CO_2 (Nagy 1983b).

Energy budget

The daily resting energy (DRE) of males and females during breeding and postbreeding seasons was calculated by multiplying the appropriate RMR (e.g., according to sex, season, temperature, and photophase or scotophase; Appendix 4.1) by the time that lizards spent at each temperature according to the thermal profile (Figure 4.2), and then summing the total O_2 consumed over 24 h. Thus, for each sex and season, we calculated the total O_2 consumed by resting lizards at night (11 h * scotophase RMR at 23ºC) and by inactive, alert lizards during the day (2 h * photophase RMR at 23ºC + 3 h * photophase RMR at 28ºC + 8 h * photophase RMR at 33ºC). Total volumes of O_2 consumption were then converted to energy equivalents using the value 20.1 J/ml O_2 (Nagy 1983b).

Statistical Analyses

Using $\log_{10}$-transformed body mass as a covariate, $\log_{10}$-transformed WIRs, FMRs, and RMRs were examined for the influence of sex and season using analysis of covariance (ANCOVA: Kleinbaum et al. 1988; SAS Institute 1989). The ANCOVA compares data independently of the effect that body mass has on metabolism. Tests were considered statistically significant at $P < 0.05$. Residuals for the data sets were normally distributed (Shapiro-Wilks statistic; W = 0.32 - 0.74). Statistical analyses were performed with SAS® release 6.12 (SAS Institute Inc., Cary, NC, 1989-1996), and power tests (i.e., the minimum detectable effect for a statistical power of 0.8; Zar 1984) for ANCOVA comparisons were performed with JMP IN® version 3.2.1 (SAS Institute Inc., Cary, NC, 1989-1997).

Results

Resting metabolic rates

Average mass-specific RMRs of males and females were, respectively: 0.242 ml O_2/g/h and 0.273 ml O_2/g/h at 28°C during the breeding season, 0.279 ml O_2/g/h and 0.352 ml O_2/g/h at 33°C during the breeding season, and 0.352 ml O_2/g/h and 0.365 ml O_2/g/h at 28°C during the postbreeding season (Table 4.1, Figs. 4.3 and 4.4). Within each temperature and season, sex had no influence on RMRs (ANCOVA; neither slopes nor intercepts significantly differed, $P > 0.90$). Thus, differences in male and female mass-specific RMRs (i.e., ml O_2/g/h; Table 4.1) are due to males having a 40% greater body mass than females and the allometric effect of body mass on metabolism.

The RMRs measured during the breeding season at 33°C were substantially, but not significantly, higher than those measured at 28°C (by 15% for males, and 29% for females; Table 4.1, Fig. 4.3) (ANCOVA, data for both sexes pooled; for the intercepts $P = 0.07$, for the slopes $P = 0.35$). The insignificant statistical result may have been due to the small sample size of measurements at 33°C ($n = 7$). The Q10 for the temperature interval of 28 - 33°C was 1.3 for males, and 1.7 for females (Appendix 4.1). The RMRs measured during the postbreeding season at 28°C were significantly higher than those measured during the breeding season at 28°C (by 45% for males, and 34% for females; Table 4.1, Fig. 4.4) (ANCOVA, data for both sexes pooled; for the intercepts $P = 0.0001$, slopes did not significantly differ, $P = 0.96$).

Since there was a different relationship between body mass and RMR for each temperature and season, three separate regressions were calculated: 1) for lizards at 28°C during the breeding season (ml O_2/day = 0.29 body mass$^{0.91}$; $R^2 = 0.72$, $F_{1,15} = 38.11$, $P = 0.0001$; Figs. 4.3 and 4.4); 2) for lizards at 33°C during the breeding season (ml O_2/day = 0.49 * body mass$^{0.68}$; $R^2 = 0.70$, $F_{1,7} = 11.90$, $P = 0.02$; Fig. 4.3); and, 3) for lizards at 28°C during the postbreeding season (ml O_2/day = 0.39 * body mass$^{0.92}$; $R^2 = 0.54$, $F_{1,15} = 34.35$, $P = 0.0001$; Fig. 4.4).

Water influx rates

Average mass-specific WIRs ranged from 0.12 - 0.14 ml/g/day (Table 4.1). Neither sex nor season had a significant influence on WIRs (ANCOVA, for the slopes and intercepts all $P > 0.051$). Pooling data for both sexes and seasons, a significant relationship between body mass and WIR is described by the equation: ml/day = 0.229 * body mass$^{0.58}$ ($F_{1,34} = 27.33$, $R^2 = 0.45$, $P < 0.0001$).

Field metabolic rates

Average mass-specific FMRs ranged from 8.5 - 10.3 ml CO_2/g/day (Table 4.1). Neither sex nor season had a significant influence on FMRs (ANCOVA, for the slopes and intercepts all $P > 0.25$). However, there was a significant relationship between body mass and FMR, described by the equation: ml CO_2/day = 13.49 body mass$^{0.71}$. After converting FMRs to energy equivalents (25.7 J/ml CO_2; Nagy 1983b), the relationship between body mass and daily field energy (DFE) is described by the equation: J/day = 348 * body mass$^{0.71}$ ($F_{1,34} = 27.10$, $R^2 = 0.44$, $P < 0.0001$; Fig. 4.5).

Energy budgets

Daily energy budgets were calculated for an average-sized male and female based on the mean (± SD) body masses of the 47 males (5.7 ± 1.08 g) and 44 females (3.3 ± 0.54 g) used in this study. The temperature, season, and phase-specific RMRs used to calculate DRE are in Appendix 4.1. For both sexes and seasons, DFE was partitioned into DRE and DAE (Figs. 4.1 and 4.6). For a male, DFE was nearly equal during both seasons (1280 J/day and 1245 J/day, respectively), whereas DRE increased 45% (661 J/day versus 961 J/day) and DAE decreased 54% (619 J/day versus 284 J/day) from breeding to postbreeding seasons (Fig. 4.6). For a female, DFE decreased 12% (874 J/day versus 766 J/day, respectively), DRE increased by 34% (459 J/day versus 614 J/day, respectively), and DAE decreased by 63% (415 J/day versus 152 J/day, respectively) from breeding to postbreeding seasons (Fig. 4.6).

Because most lizards maintained constant body mass during the 4 - 12 day sample periods (T-tests, $P > 0.17$), we assumed that energy allocated to production as growth or fat stores during these periods was zero for both sexes. Since neither sex allocated energy to growth or fat stores, total metabolizable energy (TME) was equal to DFE for males during both seasons (1280 J/day during the breeding season, and 1245 J/day during the postbreeding season), and for females during the postbreeding season (766 J/day). For females during the breeding season, we calculated TME as DFE plus the energy allocated to egg production (1365 J/day). Energy allocated to eggs was calculated as follows. Although a caloric value for *Anolis* eggs has not been determined, extensive data on many lizards indicates the energy content of eggs varies little among species (Vitt 1978). The average value for the caloric content of a lizard egg (6.537 cal/mg dry mass; Vitt 1978) was multiplied by the mean dry mass of an *A. carolinensis* egg (154 cal/mg mean dry mass, based on a mean wet mass of 293 mg for eggs laid by females collected at our study site; M. Lovern, unpublished data). One egg contains 1007 cal or 4.21 kJ, so 14 eggs produced by a 3.3 g (~52 mm SVL) female over the four-month breeding season (Andrews 1985; Michaud 1990) equate to 491 J/day, or 58.9 kJ for the entire season.

The majority of energy expended by males for reproduction is for reproductive activity (e.g., territorial advertisement and defense, competitive consexual interactions, courtship and mating), since males presumably allocate minimal energy to sperm and ejaculate production. Furthermore, *A. carolinensis* is an ambush-predator, so we assumed that the amount of energy allocated to foraging during the breeding season was also negligible for both sexes. For example, during the breeding season, males forage for food only 1% of their day (Jenssen et al. 1995a) and females forage only 1.5% of their day (Nunez et al. 1997). Therefore, the energy males allocate to reproduction was estimated as DAE during the breeding season. A 5.7 g male (~ 62 mm SVL) would allocate about 619 J/day (Fig 4.6) or 74 kJ/season to reproduction.

Females allocate energy for reproduction to eggs, and to reproductive activity (e.g., courtship, copulation, competitive consexual interactions). Thus, we estimated the energy females allocate to reproduction as the energy contained in eggs (491 J/day; see above) plus DAE during the breeding season (415 J/day; Fig. 4.6). A 3.3 g (~ 52 mm) female would allocate about 906 J/day to reproduction, or 108.7 kJ over the 4-month breeding season.

Discussion

Resting metabolic rates

Although the RMRs of *A. carolinensis* were not influenced by sex, they were significantly influenced by body mass, temperature, and season. The influence that body mass and temperature had on RMRs was similar to that reported previously for *A. carolinensis*. The average RMR we obtained in freshly-captured lizards during the breeding season (0.32 mL O_2/g/h at 33ºC) was essentially the same as that of fed *A. carolinensis* during the spring (0.34 mL O_2/g/h at 32ºC) by Licht and Jones (1967). The increase in metabolism over the temperature interval of 28 - 33ºC (Q10 of 1.5; Appendix 4.1) was also very similar to that for *A. carolinensis* during the winter (Q10 of 1.4; Jenssen et al. 1996). And finally, the influence that body mass (i.e., scaled to an exponent of 0.7 - 0.9 depending on temperature and season) and temperature had on RMRs was about the same as reported for other anoles (McManus and Nellis 1973; Bennett and Gorman 1979) and other non-*Anolis* lizards (Andrews and Pough 1985).

We found a significant 45% and 34% increase in respective male and female RMRs from breeding to postbreeding season (Table 4.1, Fig. 4.4), which we suggest is due to a threefold increase in food intake during the postbreeding season (Jenssen et al. 1995a; Nunez et al. 1997). The increase in metabolic rate that is associated with increased food intake is known as specific dynamic action (SDA), and is thought to be due to energetic costs of food handling, digestion, transport and storage of nutrients, and protein synthesis (Secor and Phillips 1997). Metabolic rates of lizards digesting food may be as much as 100% higher than post-absorptive lizards (Waldschmidt et al. 1987; Niewiarowski and Waldschmidt 1992; Secor and Phillips 1997). The RMRs of *A. carolinensis* at 28ºC and within 24 h of capture, while lizards were presumably digesting food, were 32% and 84% higher (breeding and postbreeding season, respectively) than metabolic rates of post-absorptive *A. carolinensis* (0.195 ml O_2/h; Jenssen et al. 1996). The seasonal increase in RMRs corresponds well to the seasonal increase in *A. carolinensis* feeding rates; there was a 32% difference in metabolism for post-absorptive lizards and lizards consuming 1.2 items/h during the breeding season, and an 84% difference for post-absorptive lizards and lizards consuming 3.6 items/h during the post-breeding season. The differences in *A. carolinensis* post-absorptive metabolic rates versus breeding and postbreeding RMRs are also similar to those obtained in other lizard species (Anderson and Karasov 1988; Benabib and Congdon 1992; van Marken Lichtenbelt et al. 1993). Increased feeding rates were similarly associated with a 20 - 38% increment in *Sceloporous virgatus* RMRs from breeding to postbreeding season (determined within 30 h of capture; Merker and Nagy 1984), and may have contributed to a 24 - 30% increase in *Callisaurus draconoides* FMRs (Karasov and Anderson 1998). The latter study did not find seasonal differences in RMRs, perhaps because lizards were maintained in captivity for several weeks prior to measurements.

The postbreeding increase in *A. carolinensis* food intake is probably not due to a seasonal difference in food or water availability, as insects and water were abundant at our study site during both breeding and postbreeding seasons. Rather, the food intake of males may be limited by the time that males spend in territorial activities (about 70% of their day; Jenssen et al. 1995a). During the breeding season, males forage for food only 1% of their day, and primarily eat insects encountered during patrol ("eating on the run", Jenssen et al. 1995a). In contrast, males during the postbreeding season spend three times as much time foraging, actively search for food more frequently, and feed three times more often than during the breeding season (Jenssen et al. 1995a). After four months of reproductive activity, loss of body mass indicates that territorial males may expend energy at rates exceeding their energy intake (Ruby 1984). Increased feeding rates during the postbreeding season would restore energy deficits, provide energy for growth, and provide energy stores for lizards that are inactive and primarily fast during cold winters (Jenssen et al. 1996). During the postbreeding season, both sexes have been shown to increase glycogen stores and fat body size (Dessauer 1955; Licht and Jones 1967; Wade 1981).

Since free-ranging females feed at the same rate as males during the breeding season (1.2 items/h; Nunez et al. 1997), we infer from female postbreeding increases in RMRs, glycogen stores, and fat body size (Dessauer 1955; Licht and Jones 1967; Wade 1981), that female feeding rates also increase during the postbreeding season. Previous studies have suggested that female food intake is restricted by the space that eggs take up in the body cavity (Rand 1984; van Marken Lichtenbelt et al. 1993; Weeks 1996). Other studies have suggested that gravidity contributes to reduced mobility and decreased foraging efficiency, and/or increases susceptibility to predators, causing females to forage less often (Sinervo et al. 1991; studies reviewed by Schwarzkopf 1994). Although female *A. carolinensis* are relatively inactive during the breeding season (e.g., < 14 displays/h, travel < 4 m/h , consexual interactions about once a day, Nunez et al. 1997; Jenssen and Nunez 1998), the reasons for their inactivity and presumed low food intake during this time are difficult to identify. While it's possible that females carrying eggs may restrict activity to conserve energy or reduce susceptibility to predators, it may also be that they simply do not need to be active. If *A. carolinensis* females are physiologically limited in how quickly they can produce eggs, and if energy intake above a certain level does not increase reproductive output, then a modest feeding rate may meet female energy needs during the breeding season.

Water influx rates

The WIRs of *A. carolinensis* were primarily influenced by body mass (Table 4.1). Comparison of *A. carolinensis* WIRs with the estimated water content of food (the amount of food required to support the DFE; Appendix 4.2) suggests that as much as 70% of water influx was due to lizards drinking water. At our temperate study site, *A. carolinensis* have water available as morning dew, from the adjacent Augusta Canal, or the nearby Augusta River. Consistent with a lizard that has free access to water, *A. carolinensis* WIRs (0.12 - 0.14 ml/g/day) were similar to those of tropical lizards (0.12 ml/g/day for both *Lacerta viridis*, Bradshaw et al. 1987, and *Sceloporus variabilis*, Benabib and Congdon 1992).

Field metabolic rates

The FMRs of *A. carolinensis* were primarily influenced by body mass, and did not significantly differ by sex or season (Table 4.1, Fig. 4.5). However, it can be difficult to detect sex or seasonal differences in FMRs, due to the high variance in doubly-labeled water data. Although male FMRs were similar during both seasons, the average female FMR decreased by 12% from breeding to postbreeding seasons (Table 4.1). However, a post-hoc power test on our data revealed that we only had statistical power (0.8) to detect about a 15% difference in FMRs. Perhaps due in part to low statistical power, several studies have also reported a lack of significant sex or seasonal differences in FMRs (e.g., *Agama impalearis*: Zari and Nagy 1997; *Amblyrhynchus cristatus:* Nagy and Shoemaker 1984; *Callisaurus draconoides*: Karasov and Anderson 1998; *Iguana iguana*: van Marken Lichtenbelt et al 1993; and *Sceloporus occidentalis*: Bennett and Nagy 1977). Large sample sizes may be required to increase statistical power and detect potential differences in FMRs.

As a temperate species with ample food and water availability, it is to be expected that *A. carolinensis* FMRs should be higher than those of resource-limited species, and similar to those of other temperate lizards. Although *A. carolinensis* FMRs (218 - 265 J/g/day) were within the range of those reported for other lizards (e.g., 58 - 437 J/g/day; Nagy 1999), they were most similar to those of tropical and temperate lizards (e.g., *L. viridis*, 227 J/g/day, Bradshaw et al. 1987; *S. variabilis*, 240 J/g/day, Benabib and Congdon 1992; *Lophognathus temporalis*, 209 J/g/day, Christian et al. 1999). The influence that body mass had on *A. carolinensis* FMRs was body mass scaled to an exponent of 0.71 (Figure 4.5), which is similar to the average exponent of 0.78 reported for other Iguanid lizards (Nagy 1999), and lower than the average exponent of 0.93 reported for desert lizards (Nagy 1999).

Energy budget hypotheses

Our first hypothesis H_1, that males and females allocate about an equal amount of energy to reproduction was not supported. Based on the energy budgets we calculated for *A. carolinensis* during the breeding season, a 3.3 g female would allocate about 46% more energy than a 5.7 g male to reproduction (Fig. 4.6). For an entire four-month breeding season, males would allocate about 74 kJ to reproductive activity, while females would allocate about 109 kJ to reproductive activity and egg production. That female *A. carolinensis* invest 46% more total energy in reproduction than males is surprising, given that males are 40% larger in body mass and have much greater activity levels than females. It is possible that males have less energy available for reproduction than females. Due to the time required for territorial activities, males spend little time foraging (1% of their day; Jenssen et al. 1995a). Loss in male body mass by the end of the 4-month breeding season (Ruby 1984; Jenssen 1995b) also indicates that food intake may not meet male energy needs. Reduced foraging and energy deficits may contribute to an apparent 75% mortality rate for territorial males by the end of the 4-month breeding season (Ruby 1984), which constitutes an additional and important cost of reproduction for males (Trivers 1972; Schwarzkopf 1994).

Because *A. carolinensis* females allocate more energy than males to reproduction, and because polygynous males produce more offspring than females, females also allocate more energy to individual offspring than males. A female producing 14 eggs would allocate about 7.8 kJ/hatchling. Assuming a territorial male has three resident females and successfully defends his territory from other males for the entire four-month breeding season, he would sire about 42 offspring and allocate only 1.8 kJ/hatchling. Even a more conservative estimate of male reproductive success, that a male sires 70% of the offspring produced by his resident females, would result in a male allocating only about 2.5 kJ/hatchling. In contrast to monogamous males and females that may allocate about the same amount of energy to individual offspring, that *A. carolinensis* males invest less energy in individual offspring than females is consistent with expectations for a polygynous mating system (Bateman 1948; Trivers 1972).

Our second hypothesis H_2, that males expended greater energy for activity (DAE) than females during the breeding season, was supported. The energy budgets indicate that males allocated about 50% more energy to daily activity than females during the breeding season (Fig. 4.6). The disparity in male and female DAE is consistent with the difference in their activity levels; rates of display and movement average 100 displays/h and 26 m/h for males, and 14 displays/h and 4 m/h for females. That males also expended 44% more daily resting energy than females during the breeding season (Fig. 4.6) is due to males having greater body mass than females because both sexes have similar RMRs after adjusting for differences in body mass (Fig. 4.4). Both sexes expended a similar amount of total maintenance energy (TME) during the breeding season (within 7%, Fig. 4.6).

Our third hypothesis H_3, that both sexes would expend greater total maintenance energy (TME) during the breeding season than during the postbreeding season, was supported only for females. Females during the breeding season expended about 80% more TME than during the postbreeding season, whereas males expended about the same amount of TME during both seasons (Fig. 4.6). The difference in male and female TME during the postbreeding season was due primarily to males having a 40% larger body mass than females because both sexes had similar rates of DFE after adjusting for differences in body mass (Fig. 4.5). The seasonal decrease in female TME coincides with the cessation of egg production and decreased DAE during the postbreeding season. Both sexes had a dramatic seasonal decrease in DAE (54% for males and 63% for females), and a large seasonal increase in DRE from breeding to postbreeding seasons (45% for males and 34% for females; Fig. 4.6). The decrease in male DAE is consistent with the shift from intense territorial activity during the breeding season to greatly reduced activity during the postbreeding season. For example, mean display and travel rates decrease from 100 displays/h and 26 m/h during the breeding season to 6 displays/h and 8 m/h during the postbreeding season (Jenssen et al. 1995a). For both sexes, the seasonal increase in DRE was a result of the seasonal increase in RMRs, which we attributed to increased food intake and specific dynamic action.

Comparison with other lizard species

To date, there have been only six studies that examined energy expenditure in reproductive lizards (*Sceloporus jarrovi*, Congdon 1977; *Sceloporus occidentalis*, Bennett and Nagy 1977; *Uta stansburiana*, Nagy 1983b; *Cnemidophorus tigris*, Anderson and Karasov 1988; *Iguana iguana*, van Marken Lichtenbelt et al. 1993; *Callisaurus draconoides*, Karasov and Anderson 1998), two of which did not estimate the energy expended by each sex for reproduction. For the four studies that did report this information, we made a standardized comparison by calculating the energy expended for reproduction as male DAE during the entire breeding season, and female DAE during the entire breeding season + energy allocated to egg production (Table 4.2). Similar to the results of our study, that females allocated more energy for reproduction than males, the amount of energy allocated by females for reproduction exceeded that of males by 44% in *S. occidentalis*, 110% in *U. stansburiana*, and 234% in *I. iguana*. Only *S. jarrovi* males expended more energy for reproduction than females, and that difference was only 11% (Table 4.2). Thus, despite the high activity rates of territorial males, females appear to allocate more energy for reproduction than males in most lizard species examined. As with *A. carolinensis*, males may simply be more limited than females in the amount of food they can consume, and may also have increased mortality as a consequence of the energy and time devoted to reproduction.

The amount of energy expended for reproduction is influenced by many factors, including ecology, reproductive strategies, foraging habits, and life history traits. *Anolis carolinensis* is temperate, has a polygynous and territorial mating strategy, and is an insectivorous ambush-predator. With the exception of *C. tigris* and *I. iguana*, the lizard species in Table 4.2 are also polygynous, territorial, and insectivorous ambush-predators, but they live in arid/semi-arid habitats. *Cnemidophorus tigris* is a polygynous, desert, insectivore, but both sexes employ a wide-searching strategy for finding food and mates. *Iguana iguana* is a tropical herbivore with a territorial mating strategy and an active-search foraging strategy. To facilitate comparisons among these species, we calculated the total maintenance energy expended during the breeding season and the amount of energy allocate to eggs by females for *A. carolinensis* and the six other species (Table 4.2). After adjusting for interspecific differences in body size (energy expenditure/body mass$^{0.8}$; Nagy 1999), the TME of male *A. carolinensis* for an entire breeding season was 37-180% greater than that of the four ambush-predators and 220% greater than the tropical herbivore *I. iguana*, but 27% less than the active forager *C. tigris*. Female *A. carolinensis* expended 39-378% more TME (adjusted for body size) than all six other lizard species, and allocated 11-228% more energy to eggs than all five of the arid/semi-arid species (Table 4.2). However, the proportion of TME that females allocated to egg production was similar for *A. carolinensis* (36%), *C. draconoides* (29%), *S. jarrovi* (33%), and *U. stansburiana* (36%). In contrast, *C. tigris* and *S. occidentalis* females allocated only 13% and 14% of TME to egg production, respectively (Table 4.2). The proportion of TME that female *I. iguana* allocated to egg production (47%) may be overestimated. *Iguana iguana* has a 2-month mating season from March-April (van Marken Lichtenbelt 1993), but oviposition takes place during May or June. Thus, *I. iguana* females may expend energy for reproduction over more than the two months used in our calculations, which would increase the DFE and TME for the breeding season, and result in a lower proportion of TME that females allocated to eggs.

As would be expected, *A. carolinensis* appear to have more energy available for reproduction than lizards from semiarid/desert habitats, due no doubt to plentiful food and water resources in a temperate habitat. Water scarcity in semi-arid or desert environments not only limits primary production and prey abundance, it limits the amount of food that can be processed and/or harvested (Congdon 1989). As a result of abundant resources, *A. carolinensis* males and females expend more total energy during the breeding season, and females allocate more energy to eggs, than that measured for species from semiarid/desert habitats. The one exception, *C. tigris*, is an active forager that harvests more total energy than any of the other species, including *A. carolinensis* males. However, the energy demands associated with searching for food and mates results in *C. tigris* females allocating less energy to eggs than the other species, including *A. carolinensis*.

Although the amount of energy that both sexes allocate to reproduction can, in part, help us to understand the various factors that influence the evolution of particular mating strategies, few studies have actually done so, perhaps because quantifying this energy expenditure can be difficult. Several aspects of life history complicate studies that attempt to measure the energy expended for reproduction. For instance, all of the lizards compared above, except for *A. carolinensis*, are ‘capital’ breeders that use at least some energy that is stored prior to breeding for reproduction (Jonsson 1997), but only two studies accounted for stored energy in their calculations (e.g., Congdon 1977; Nagy 1983b). In contrast, ‘income’ breeders (Jonsson 1997) like *A. carolinensis* rely mostly on energy obtained during the breeding season for reproduction, and quantifying this amount of energy is more straightforward than for capital breeders. Species may also have more than one breeding season and/or clutch per year, breed for one year only or for multiple years, or may vary the amount of energy expended for reproduction with age (e.g., Congdon 1977; Nagy 1983b). Clearly more studies are needed to determine how various factors impact the energy lizards expend for reproduction, and to better understand the relationships between energy expenditure, life-history traits, and mating strategies.

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Table 4.1. *Anolis carolinenis* mean snout vent lengths (SVL), body masses, resting metabolic rates (RMRs), water influx rates (WIRs), and field metabolic rates (FMRs) during breeding and postbreeding seasons [mean (n, standard deviation)].

	Males		Females	
Breeding season RMRs at 28ºC:				
SVL (mm)	60.5	(8, 3.16)	51.2	(9, 1.13)
Body mass (g)	5.49	(8, 1.21)	3.08	(9, 0.41)
RMR (ml O_2/g/h)	0.242	(8, 0.05)	0.273	(9, 0.05)
Breeding season RMRs at 33ºC:				
SVL (mm)	62.6	(5, 3.72)	52.0	(2, 2.00)
Body mass (g)	6.16	(5, 1.46)	2.80	(2, 0.64)
RMR (ml O_2/g/h)	0.279	(5, 0.07)	0.352	(2, 0.07)
Postbreeding season RMRs at 28ºC:				
SVL (mm)	62.2	(17, 3.33)	52.5	(14, 3.83)
Body mass (g)	5.76	(17, 1.16)	3.46	(14, 0.65)
RMR (ml O_2/g/h)	0.352	(17, 0.09)	0.365	(14, 0.08)
Breeding Season WIRs and FMRs:				
SVL (mm)	63.1	(7, 3.72)	52.2	(10, 1.72)
Body mass (g)	5.94	(7, 1.30)	3.29	(10, 0.36)
WIR (ml H_2O/g/day)	0.12	(7, 0.02)	0.14	(10, 0.03)
FMR (ml CO_2/g/day)	8.74	(7, 1.85)	10.30	(10, 1.94)
Postbreeding Season WIRs and FMRs:				
SVL (mm)	61.6	(10, 1.96)	53.4	(9, 3.06)
Body mass (g)	5.55	(10, 0.65)	3.52	(9, 0.55)
WIR (ml H_2O/g/day)	0.12	(10, 0.03)	0.13	(9, 0.02)
FMR (ml CO_2/g/day)	8.50	(10, 2.64)	9.03	(9, 2.01)

Table 4.2. The daily field energy (DFE), energy allocated to egg production, energy allocated to reproduction, and total maintenance energy (TME) expended for an entire breeding season (values are per season unless otherwise indicated) by males (M) and females (F) of seven lizard species.

		Mass	BSD[a]	DFE		Eggs	Reproduction[b]	TME[c]	
Species	Sex	(g)	(days)	(J/day)	(kJ)	(kJ)	(kJ)	(kJ)	(kJ/g$^{0.8}$)
Anolis carolinensis	M	5.7	120	1280	154	-	74	154	38.3
	F	3.3		874	105	59	109	164	63.1
Callisaurus draconoides[d]	M	10.5	120	1403	168	-	-	168	25.6
	F	8.0		1100	132	53	-	185	35.1
Cnemidophorus tigris[e]	M	18.8	90	5628	507	-	-	507	48.5
	F	15.8		4009	361	52	-	413	45.4
Iguana iguana[f]	M	713.0	60	55329	3320	-	1892	3320	17.3
	F	1004.0		72188	4331	3847	6317	8178	32.5
Sceloporus jarrovi[g]	M	23.9	61	2860	174	-	40	174	13.7
	F	17.4		1427	87	43	36	130	13.2
Sceloporus occidentalis[h]	M	11.9	120	1549	186	-	105	186	27.9
	F	11.9		1666	200	32	151	232	32.3
Uta stansburiana[i]	M	3.7	117	551	64	-	22	64	22.5
	F	2.4		271	32	18	50	45	24.8

[a] BSD = breeding season duration.

[b] Energy allocated to activity by males, and energy allocated to activity + eggs for females.

[c] TME = DFE/season + energy allocated to eggs. We calculated TME/body mass$^{0.8}$ to adjust for interspecific differences in body size (Nagy 1999).

[d] Karasov and Anderson 1998.

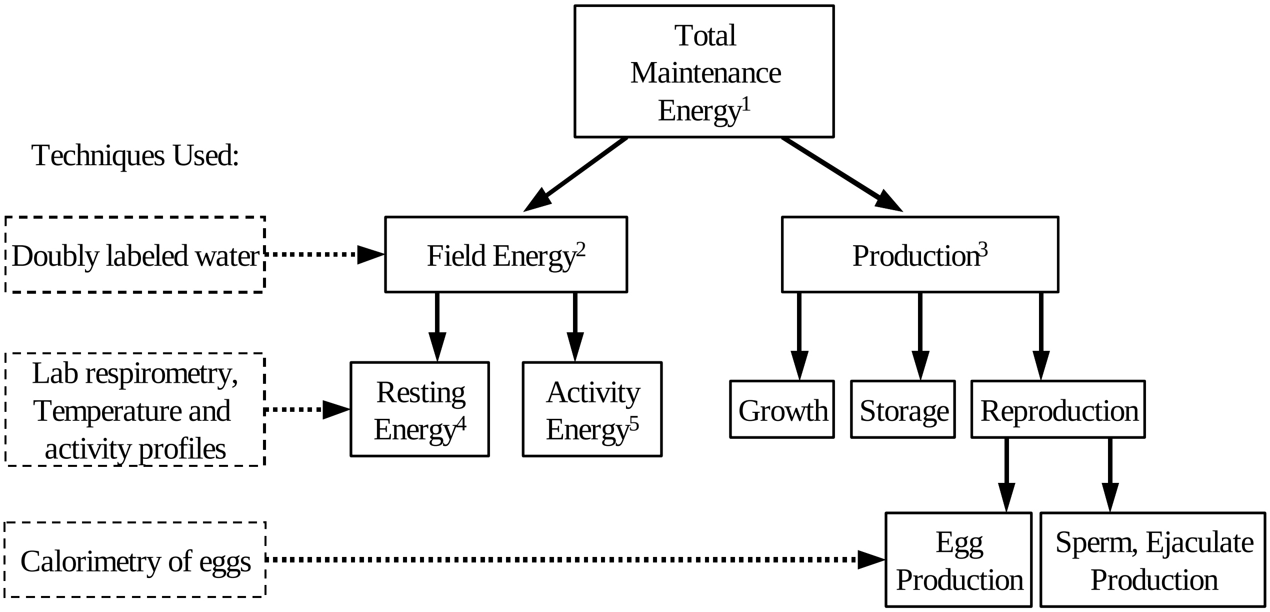
[e] Anderson and Karasov 1988.

[f] van Marken Lichtenbelt et al. 1993 (since oviposition takes place 1-2 months after the breeding season, females may expend more DFE and TME than indicated above).

[g] Congdon 1977 (Turkey Creek population).

[h] Bennett and Nagy 1977 (BSD from Stebbins 1985).

[i] Nagy 1983b.



Definitions for terms:

[1]**Total maintenance energy** (TME): total energy assimilated by an individual per unit time. Partitioned into energy allocated to field energy and production.

[2]**Field energy** (daily field energy or DFE): total energy expended by free-ranging lizards, measured as volume of CO_2 expired per h or per day and converted to joules using energy coefficients. Partitioned into energy allocated to resting and activity.

[3]**Production**: total energy allocated to production. Partitioned into energy allocated to growth (lean somatic tissue), storage (lipid deposition), and reproduction (gametes, egg production).

[4] **Resting energy** (daily resting energy or DRE): the proportion of field energy expended while resting (sleeping or inactive), calculated from temperature-specific, resting metabolic rates measured in absorptive subjects (i.e., digesting food) and temperature and activity profiles of free-ranging subjects.

[5]**Activity energy** (daily activity energy or DAE): the proportion of field energy allocated to activity, calculated by subtracting resting energy from field energy. Includes energy allocated to activities such as: territory defense, courtship, copulation, laying eggs, foraging and thermoregulation.

Figure 4.1. Schematic diagram for the partitioning of an energy budget, techniques used in this study to obtain data, and definitions for the terms and associated acronyms used in the text.

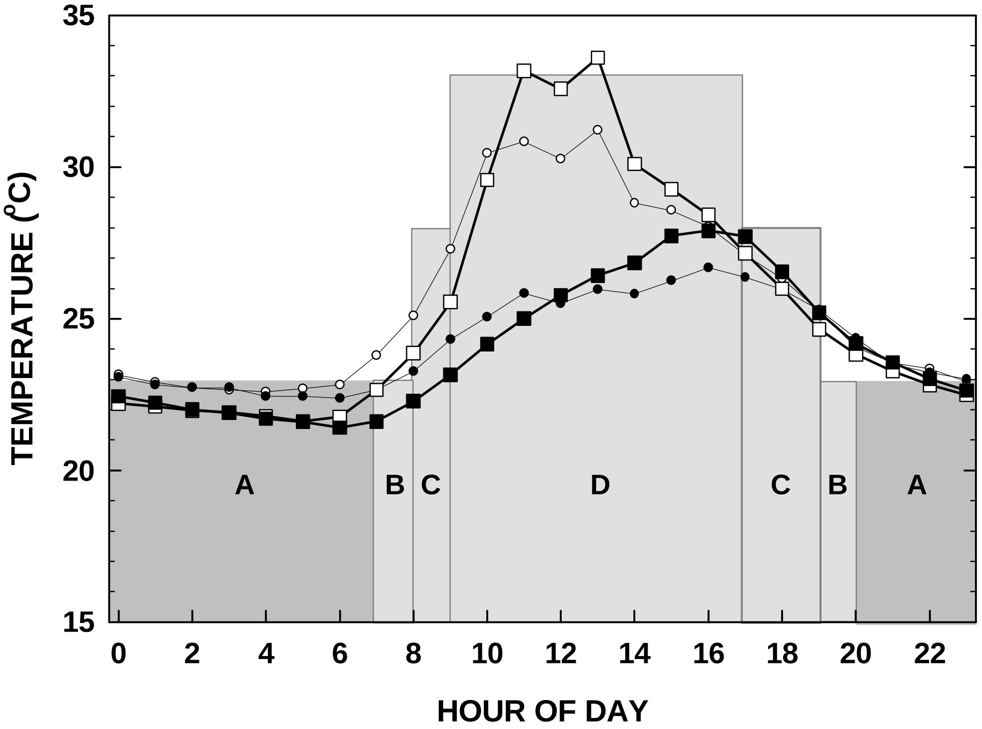


Figure 4.2. Mean air temperatures recorded hourly at the Augusta Canal study site Augusta, GA, during the breeding season (thin lines) at sunny (") and shaded (!) locations, and during the postbreeding season (thick lines) at sunny (Q) and shaded (#) locations. Areas with gray fill represent the estimated daily thermal profile for *Anolis carolinensis*, which is composed of four periods: **A -** lizards asleep during the scotophase (nighttime, ■) for 10 h at 23°C (body temperature of lizards estimated to be the same as average air temperature), **B -** lizards alert or active for 2 h during the photophase (daytime, □) at 23°C (body temperature of lizards estimated to be the same as average air temperature), **C -** lizards active for 3 h during the photophase at 28°C (average body temperature of lizards estimated for the transition from 23°C to 33°C), and **D -** lizards active for 8 h during the photophase at 33°C (body temperature measured in 16 active lizards).

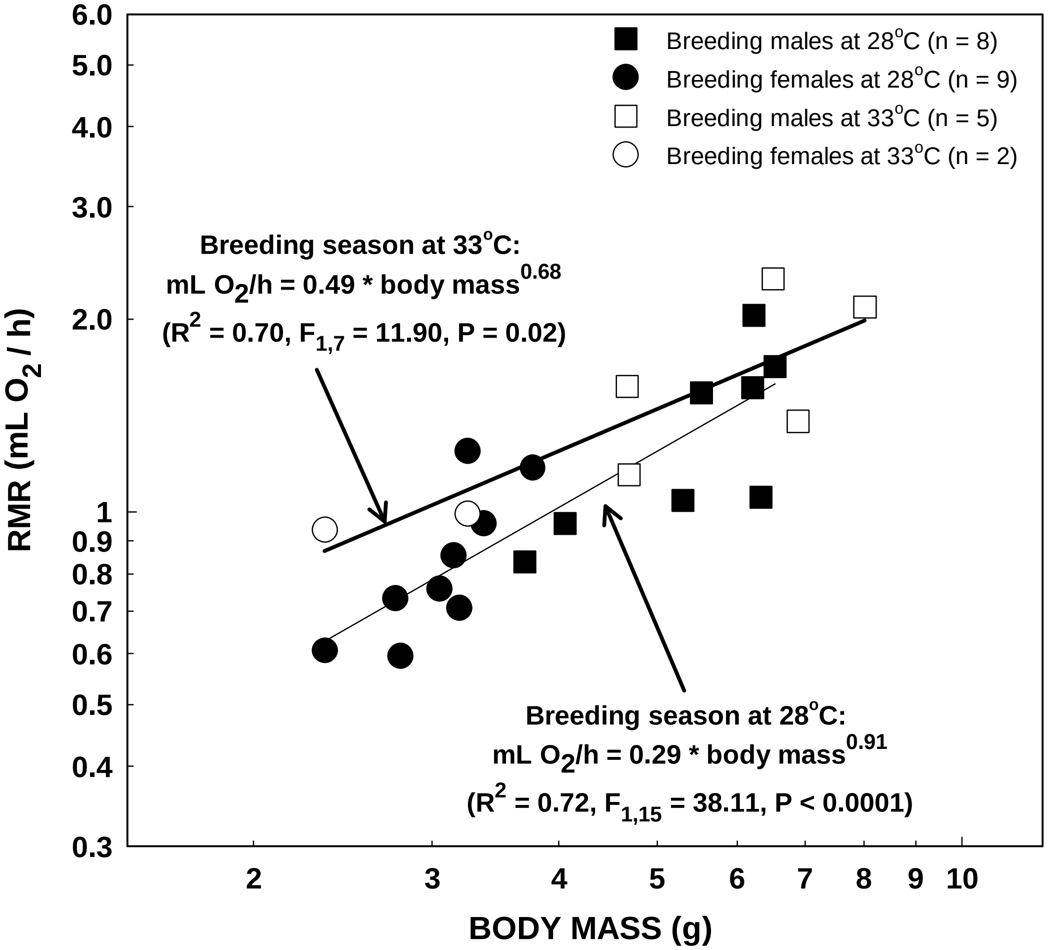


Figure 4.3. Resting metabolic rate (RMR) as a function of body mass for *Anolis carolinensis* measured during the breeding season at 28°C (males - **Q**, females - **"**) and at 33°C (males - **#**, females - **!**). Lines indicate least-squares linear regression for the breeding season at 28°C (——) and at 33°C (━━).

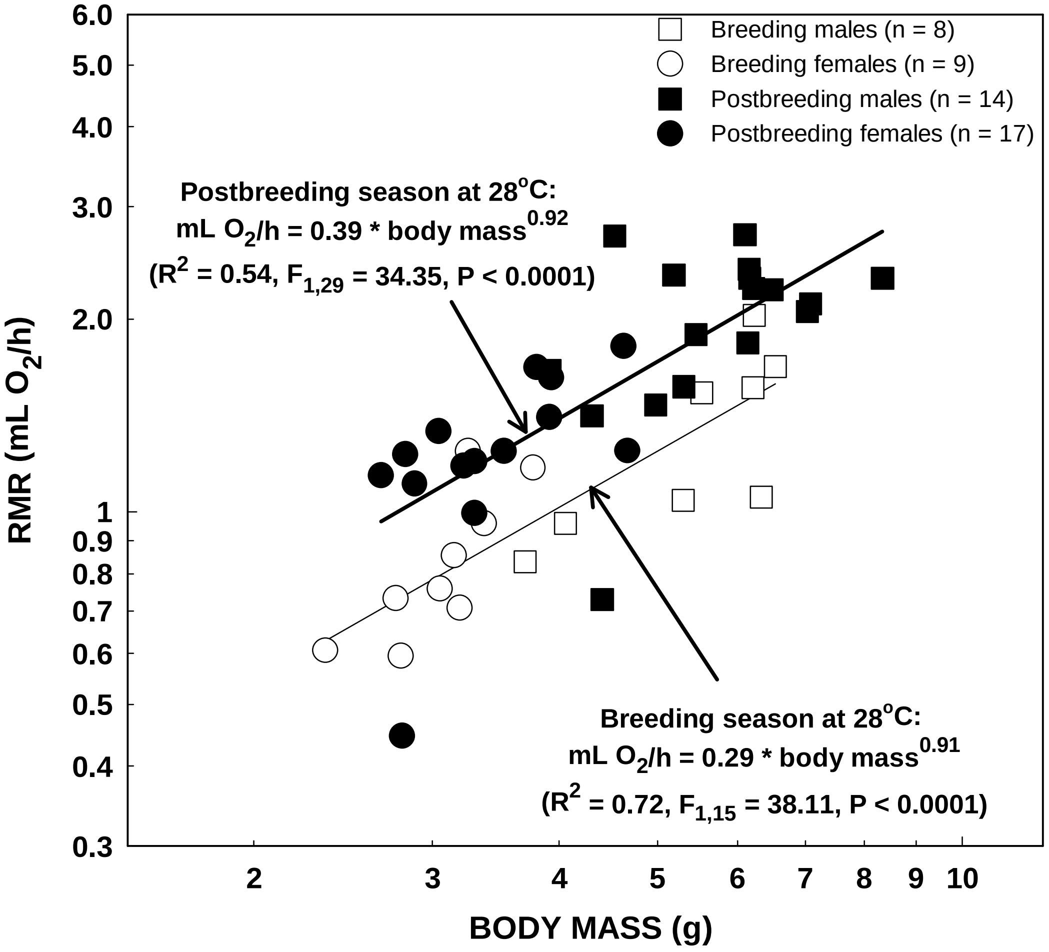


Figure 4.4. Resting metabolic rate (RMR) as a function of body mass for *Anolis carolinensis* measured at 28°C during breeding (males - **Q**, females - **"**) and postbreeding (males - **#**, females - **!**) seasons. Lines indicate least-squares linear regression for breeding (——) and postbreeding (**——**) seasons.

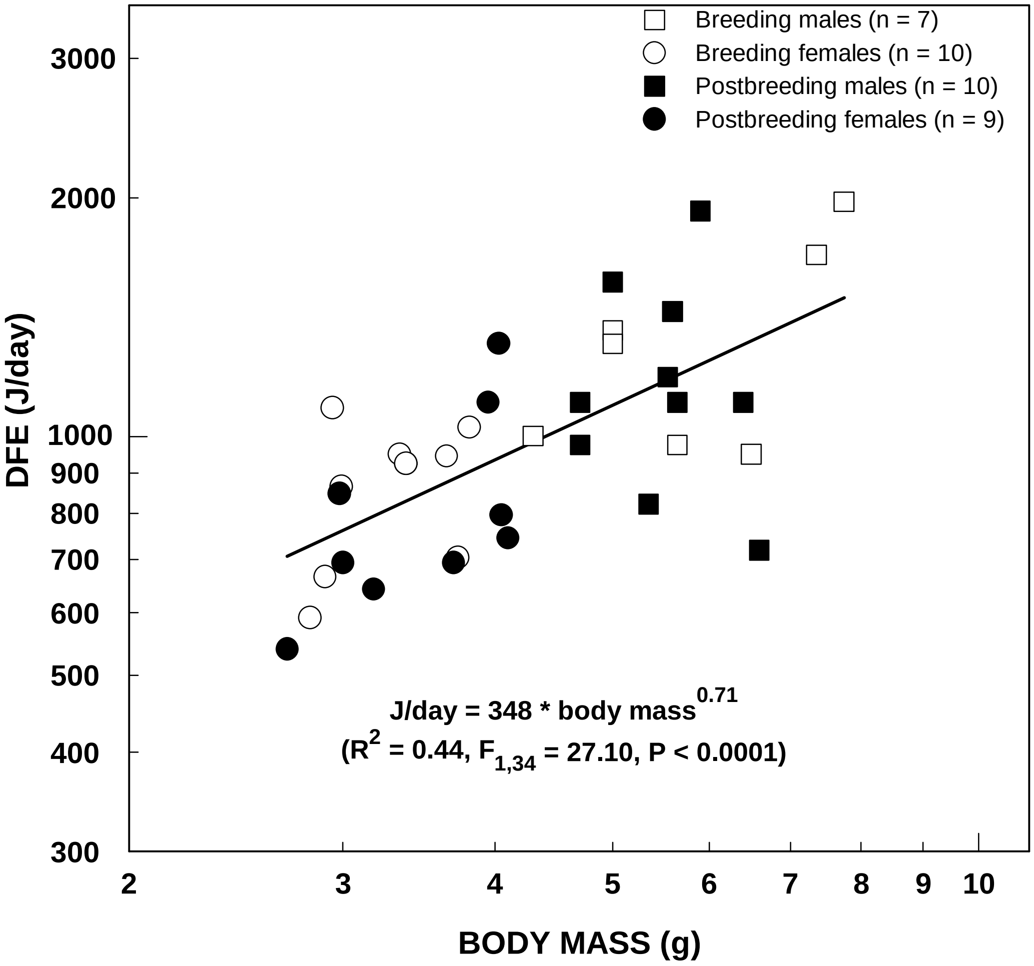


Figure 4.5. Daily field energy (DFE) as a function of body mass for *Anolis carolinensis* during the breeding (males - **Q**, females - **"**) and postbreeding (males - **#**, females - **!**) seasons. Line indicates the least-squares linear regression for all data.

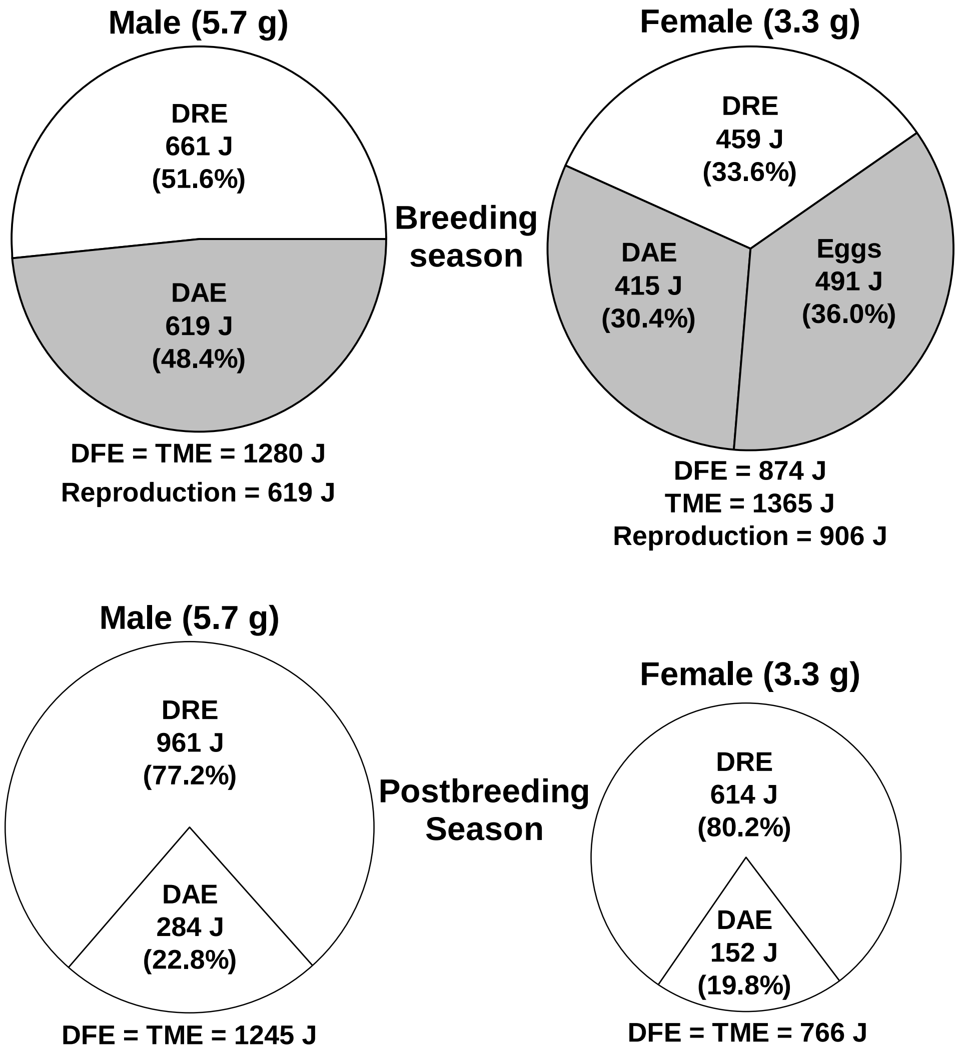


Figure 4.6. Estimated daily energy budgets for male and female *Anolis carolinensis* during breeding and postbreeding seasons. Pie size reflects the relative amount of total maintenance energy (TME) expenditure for each sex and season. Total maintenance energy = daily field energy (DFE; determined by the doubly labeled water technique) + the energy allocated to eggs, storage, and/or growth (energy allocated to storage and growth during the study periods was zero). Daily resting energy (DRE) was calculated from resting metabolic rates and a time-temperature profile. Daily activity energy (DAE) = DFE - DRE. Proportion of TME allocated to reproduction during the breeding season (DAE for males, and DAE + egg production for females) indicated by gray fill (■). See Fig. 4.1 and text for details of calculations.

Appendix 4.1. Resting metabolic rates (RMRs) for *Anolis carolinensis* males and females at three different temperatures, during breeding and postbreeding seasons, and during the scotophase (sleeping during the night) and photophase (awake and alert during the day).

	RMR (ml O_2/g/h)		
	23°C	28°C	33°C
Males:			
Breeding season, scotophase:	0.118[a]	0.242[b]	0.279[b]
Breeding season, photophase:	0.165[c]	0.339[c]	0.391[c]
Postbreeding season, scotophase:	0.172[d]	0.352[b]	0.406[e]
Postbreeding season, photophase:	0.240[c]	0.493[c]	0.568[c]
Females:			
Breeding season, scotophase:	0.133[a]	0.273[b]	0.352[b]
Breeding season, photophase:	0.186[c]	0.381[c]	0.493[c]
Postbreeding season, scotophase:	0.178[d]	0.365[b]	0.472[e]
Postbreeding season, photophase:	0.249[c]	0.511[c]	0.661[c]

[a] Rates estimated from the Q10 value for the temperature interval 23–28°C = 4.21 (Q10 based on *A. carolinensis* winter standard metabolic rates, data reported by Jenssen et al., 1996) and from breeding season RMRs measured at 28°C by the present study.

[b] Rates measured by the present study using laboratory respirometry.

[c] Photophase rates estimated as 1.4 times the respective scotophase rate (Andrews and Pough 1985; Beaupre et al. 1993; van Marken Lichtenbelt et al. 1993).

[d] Rates estimated from the Q10 value for the temperature interval 23–28°C = 4.21 (Q10 based on *A. carolinensis* winter standard metabolic rates, data reported by Jenssen et al., 1996) and from postbreeding season RMRs measured at 28°C by the present study.

[e] Rates estimated from the Q10 value for the temperature interval 28–33°C = 1.3 for males, or 1.7 for females (Q10 based on *A. carolinensis* breeding season RMRs), and from postbreeding season RMRs measured at 28°C by the present study.

Appendix 4.2. Comparison of daily water influx (WIR) with the estimated free water intake (µl/day) for a 5.7 g male *Anolis carolinensis* based on the amount of daily field energy expended during breeding and postbreeding seasons.

			Estimated from FMR				
	WIR (µl/day)	DFE (J)	Food wet mass (g)[a]	H_2O in food (µl)	Metabolic H_2O (µl)[b]	Free H_2O intake (µl)[c]	% of Season WIR
Breeding	684	1280	247	73	33	478	70%
Post-breeding	684	1245	241	168	32	484	71%

[a] Based on an insectivorous diet, and assuming that insects contain 70% water (Edney 1977) and 23 J/mg dry mass, 75% of which is metabolized (Harwood 1979).

[b] Metabolic water produced = DFE * 0.026 ml/kJ (Schmidt-Neilsen 1991).

[c] Free water intake = WIR - moisture in food - metabolic water production.

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Academic Degrees

1987. B.S., Biology, Central Michigan University, Mt. Pleasant MI.
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Professional Experience and Activity

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1988, 1993-96. Graduate student teaching assistant, Biology Dept., Virginia Tech, Blacksburg, VA.
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2001- present. Editorial Board, Caribbean Journal of Science.
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Teaching Experience

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Research Interests

Behavioral Ecology
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Grant Awards

1992. Sigma Xi, Grants-in-aid of Research, $350.
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1993. American Museum of Natural History, Teddy Roosevelt Memorial Fund, $750.
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1995-96. Oak Ridge Associated Universities, Research Travel Grant, $1630.
2000. Virginia Tech Graduate Student Association, Travel Grant, $300.

Publications

Orrell, K. S., and T. A. Jenssen. 1998. Display Behavior of *Anolis bahorucoensis*: an anole with a diminutive dewlap. Caribbean J. of Science 34(1-2):133-125.

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Non-refereed

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Orrell, K. S. (presenter), and T. Jenssen. Display behavior of *Anolis bahorucoensis*, an anole with a diminutive dewlap. Biology Department, Virginia Tech. June 1994.

Orrell, K. S. (presenter), and T. Jenssen. Mate discrimination by male *Anolis carolinensis*. Society for the Study of Amphibians and Reptiles, Univ. of Indiana, Bloomington. August, 1993.

Orrell, K. S. (presenter), and T. Jenssen. Mate discrimination by male *Anolis carolinensis*. Graduate Student Association Research Symposium, Virginia Tech. May, 1994.

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Orrell, K. S. (presenter), and T. Jenssen. Male mate choice by the polygynous lizard, *Anolis carolinensis*: a preference for novel females. Biology Department, Virginia Tech. May, 2002.