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

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Laboratory and field manipulations tested whether male *Anolis carolinensis* lizards and discriminate 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 differ significantly between baseline and resident-female sessions, nor did female behaviours differ significantly between 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 travelled 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% towards resident females to 53% towards the novel female) and the proportion of displays directed towards novel females (from 6% towards resident females to 51% towards 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.

Within a polygynous mating system, males can maximize reproductive success by monopolizing females through intermale contests or by participating in some form of mate choice. Although mate choice is traditionally associated with female-controlled mating systems, males should also have 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 labelled the 'Coolidge effect' (e.g. Dewsbury 1981), is characterized by an intense sexual interest in novel females. Males showing 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

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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 & 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 & 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 7 months (Fox 1963; Conner & Crews 1980). Given that females lay single-egg clutches at about weekly intervals (Andrews 1985; Michaud 1990) for 4 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 favour 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 towards 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 towards 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 ($\bar{X} \pm$ SD snout–vent lengths, SVL, 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, U.S.A. and brought to our laboratory at Virginia Tech. Lizards were housed in male/female pairs in cages $0.6 \times 0.6 \times 0.7$ m, H × W × L for 1–3 weeks prior to experimental manipulation; this time period ensured 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 lx (LI-COR LI-185B photometer) on a 12:12 h light:dark cycle. Inside the cages, the light cycle temperatures ranged from 28 °C to a maximum of 42 °C directly under the flood lights, and about 24 °C during the dark cycle.

Experiments took place in a plywood observation enclosure ($0.5 \times 0.7 \times 1.2$ m, H × W × L), 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 ($8 \times 5 \times 10$ 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 0.01-s increments from a time-date generator (Odetics

Table 1. List of 22 variables examined to evaluate the preference for novel female (PNF) response in male *Anolis carolinensis* during laboratory and field experiments

Laboratory	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 two or more displays sequenced less than 2 s apart
M, F	M	Volley size (e.g. volley of five successive headbob displays)
M, F	M	Position of a headbob display in a volley (e.g. first of five successive displays)
M, F	M	Distance (cm) travelled and whether travel was towards or away from another lizard
M, F	M	Number of moves made and whether moves were towards 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	—	Number of male (or female) headbob displays given with no response from the female (male)
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

M, F indicates variables examined for both sexes; M indicates variables examined only for males.

Model G-77). The videotapes were reviewed frame by frame to track 22 variables (Table 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 5 days. On the first day of a trial, a resident male/female pair was moved to the observation enclosure and left to acclimate to the new enclosure for 3 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 used as both a resident and a novel female in separate trials held at least 1 week apart. We randomized whether a female first served as a reintroduced 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

We tested the response of free-ranging males to novel females in a riparian habitat along the Augusta Canal near Augusta, Georgia, U.S.A., 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 $10\times$ 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 viewed frame by frame to track 17 variables (Table 1).

Females used for introductions were collected more than 200 m from where they were released in a trial to ensure 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 & Jenssen 1991). We addressed whether paint marking might facilitate novel female recognition by resident males by comparing male responses towards 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 2 days. On the first day of a trial, the baseline session began when the resident lizards became active (ca. 0900 hours) 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 (ca. 0830 hours). 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 ($4.0 \times 7.5 \times 8.0$ cm, H × W × L) 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

We analysed variables using descriptive statistics (mean, standard error, range), Wilcoxon matched-pairs signed-ranks, Wilcoxon two-sample, and stepwise regression procedures (SAS version 6.12, SAS Institute 1989). The Wilcoxon matched-pairs signed-ranks test is a nonparametric, distribution-free method for comparing matched pairs of samples that is not statistically affected by monotonic transformations (Hollander & Wolfe 1973). 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 α=0.05.

RESULTS

Laboratory Experiment

Female comparisons

For each trial, we combined data from the two 30-min baseline sessions (one recorded prior to the resident-female session, one recorded prior to the novel-female session) into a 60-min baseline session for comparison to resident-female sessions. Comparisons between baseline and resident-female sessions (Table 2) indicated that none of the 17 behavioural variables for females significantly differed (Wilcoxon matched-pairs signed-ranks test: T range −26.5–20, 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 re-entry 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 2) significantly differed (Wilcoxon matched-pairs signed-ranks test: T range −20.5–26.5, N=13, 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 whether 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 differed significantly between resident and novel females (Wilcoxon matched-pairs signed-ranks test: T range −44–40.5, N=16, NS; minimum detectable effect in 11 of 17 variables was <200%; Table 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 towards the male than novel females.

Females used display behaviours with similar frequencies during resident-female and novel-female sessions (Table 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 although seven of 18 females occasionally performed displays in

Table 2. Descriptive statistics ($\bar{X}$±SD, range in parentheses) for 17 variables recorded for female *Anolis carolinensis* during three types of laboratory sessions (baseline, resident-female and novel-female), and Wilcoxon matched-pairs signed-ranks (N=16) statistics for comparison of variables during resident-female versus novel-female sessions

		Laboratory session		Wilcoxon	
Female 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†	0.5±0.9 (0–3)*	0.1±0.2 (0–1)	0.7±1.4 (0–5)*	−1.5	0.50
Displays with no response	10.4±10.3 (0–31)**	8.4±9.8 (0–35)	5.9±12.3 (0–41)**	26	0.15
% Displays with 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±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 towards§	32.3±24.7 (0–100)**	29.8±17.7 (0–61)	16.1±14.0 (0–40)***	40.5	0.019
% Moves towards††	29.5±24.5 (0–100)**	23.3±12.4 (0–44)	16.6±15.0 (0–43)***	25	0.16
% Distance away‡‡	24.1±20.3 (0–57)***	31.1±15.8 (9–67)	51.2±30.4 (0–100)***	−44	0.021
% Moves away§§	23.3±19.5 (0–60)***	31.4±18.1 (7–67)	46.6±29.9 (0–100)***	−38	0.049
Total distance 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

Asterisks indicate the magnitude of statistically detectable differences (***<100%, **100–200%, *>200%) between baseline and resident-female contexts (baseline column of data), and between resident-female and novel-female contexts (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).
†Dewlap extensions or pulses given without a headbob display.
‡Comparisons performed using mean volley size for each subject and session.
§The percentage of the total distance moved that was towards the other lizard.
††The percentage of the total number of moves that were towards the other lizard.
‡‡The percentage of the total distance moved that was away from the other lizard.
§§The percentage of the total number of moves that were away from the other lizard.

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 2).

Male comparisons

For each trial, we combined data from the two 30-min baseline sessions 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 differed significantly (Wilcoxon matched-pairs signed-ranks test: T range −20–7, N=16, NS; minimum detectable effect in 17 of 22 variables was <200%; Table 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 differed significantly (following sequential Bonferroni adjustments to P values), with 14 of the 16 males displaying intensified courtship towards 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 matched-pairs signed-ranks test: T=−57, N=16, P=0.0016; Table 3). The high display rate of males towards 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 males' displays 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), 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).

Males performed significantly longer and more frequent display volleys (defined as 2 or more displays less than 2 s apart) during novel-female sessions than during resident-female sessions, averaging 3.7 versus 2.5 displays/volley, respectively (Wilcoxon matched-pairs signed-ranks test: 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). 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

Table 3. Descriptive statistics ($\bar{X}$±SD, range in parentheses) for 22 variables recorded for male *Anolis carolinensis* during three types of laboratory sessions (baseline, resident-female and novel-female), and Wilcoxon matched-pairs signed-ranks (N=16) statistics for comparison of variables during resident-female versus novel-female sessions

Male behaviours	Laboratory session			Wilcoxon	
	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†	0.3±0.7 (0–2)**	0.3±0.7 (0–2)	0.3±0.6 (0–2)*	−0.5	1.0
Displays with no response	5.9±8.1 (0–32)**	5.9±8.7 (0–25)	33.4±36.2 (0–122)*	−30	0.005
% Displays with dewlap	99.3±1.4 (96–100)***	98.4±3.4 (88–100)	98.2±3.8 (89–100)***	−1	0.95
% Displays with 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‡	2.4±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§	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 towards††	27.6±20.0 (0–70)***	30.0±20.2 (0–79)	58.0±29.9 (0–100)**	−47	0.013
% Moves towards‡‡	25.6±16.3 (0–54)***	26.3±15.8 (0–45)	55.6±29.1 (0–100)**	−51	0.006
% Distance away§§	35.4±25.7 (0–94)***	38.3±23.7 (0–100)	10.2±16.2 (0–63)***	51.5	**0.002**
% Moves away†††	37.8±26.8 (0–93)***	34.9±21.6 (0–100)	8.1±8.9 (0–29)***	60	**0.0007**
Total distance 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

Asterisks in the baseline and novel-female columns indicate the magnitude of statistically detectable differences (***<100%, **100–200%, *>200%) between baseline and resident-female sessions, and between resident-female and novel-female sessions, respectively, at a power level of 90%. Note: only *P* values in boldface were statistically significant following sequential Bonferroni adjustments (Rice 1989).
†Dewlap extensions or pulses given without a headbob display.
‡Comparisons performed using mean volley size for each subject and session.
§Total static modifiers, including: crests, lateral compressions and gular expansions.
††The percentage of the total distance moved that was towards the other lizard.
‡‡The percentage of the total number of moves that were towards the other lizard.
§§The percentage of the total distance moved that was away from the other lizard.
†††The percentage of the total number of moves that were away from the other lizard.

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). When display modifiers were used by males, the frequency of appearance for all modifiers combined was 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 nonsignificant following sequential Bonferroni P value adjustment ($T=-14$, N=16, NS, minimum detectable effect >200%; Table 3).

Males moved twice as frequently and twice the distance towards novel females as towards resident females (respective Wilcoxon matched-pairs signed-ranks test: $T=-51$ 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=51.5 and 60, N=16, P=0.002 and 0.0007, respectively; Table 3). Persistent movements of males towards novel females and less movement made away from novel females compared with 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) (Wilcoxon matched-pairs signed-ranks test: $T=-7.5$–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. As expected, male display rate was significantly correlated with the type of session (stepwise regression: $F_{1,44}$=12.31, R=0.47, P<0.001), but not with

Table 4. Descriptive statistics ($\bar{X}$±SD, range in parentheses) for six variables recorded for 18 free-ranging male *Anolis carolinensis* during baseline and novel female sessions and three types of social context

	Social context		
	Nondirected*	Resident-female	Novel-female
Baseline session			
% Time/session†	75.0±20.9 (37–100)	5.3±10.2 (0–33)	—
% Displays/session‡	94.3±6.4 (79–100)	5.7±6.4 (0–21)	—
Displays/min§	2.2±0.7 (1–4)	1.0±1.6 (0–5)	—
% Low-amplitude displays**	0.8±1.3 (0–4)	0.1±0.3 (0–1)	—
% Displays in volleys††	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†	18.8±19.1 (0–65)	1.2±2.12 (0–9)	53.2±24.3 (3–100)
% Displays/session‡	44.2±27.5 (0–86)	4.4±10.7 (0–46)	51.4±27.1 (9–100)
Displays/min§	2.9±1.6 (0–8)	0.1±0.3 (0–1)	2.0±1.1 (0–5)
% Low-amplitude displays**	0.5±1.4 (0–6)	0	7.3±14.3 (0–61)
% Displays in volleys††	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)

*Nondirected context refers to territorial activities (territorial advertisement, patrol and monitoring).
†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).
‡Proportion of all displays in a session performed during nondirected, resident-female and novel-female social contexts.
§Rate of displays/min discounting periods of time that males were not displaying.
**Proportion of displays performed as low-amplitude variants.
††Proportion of volleyed displays (two or more sequential displays less than 2 s apart).

female body mass or female display rate ($F_{1,44}$=0.07, R=0.04, NS). Similarly, female display rate was not correlated with type of session, male body mass, male display rate, or the number of shudderbobs performed by males ($F_{1,43}$=2.46, R=0.23, NS).

Field Experiment

All 18 focal males in the study altered their baseline behavioural profiles with the introduction of novel females (Table 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 matched-pairs signed-ranks test: 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 towards 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 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 matched-pairs signed-ranks test: T=84.5, N=18, P<0.0001). Displays directed towards 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 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 towards novel females were 20-fold higher than rates towards 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 towards 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 towards

novel females (novel-female sessions), but only 0.1% of displays directed towards resident females during baseline sessions (Wilcoxon matched-pairs signed-ranks test: $T=-26.5$, $N=18$, $P<0.0039$). Low-amplitude displays were used by nine of the18 males towards novel females, and by only two males towards resident females during baseline sessions.

Second, displays directed towards 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 4), and volleys performed towards novel females were significantly longer than volleys performed during nondirected territorial activity (Wilcoxon matched-pairs signed-ranks test: $T=56.5$, $N=17$, $P<0.0053$).

Third, male body colour shifted from green to brown or brown to green about twice as often during novel-female sessions as during baseline sessions (mean colour change of 3.6 times/h ± 2.6 versus 1.6 times/h ± 2.0, respectively; Wilcoxon matched-pairs signed-ranks test: $T=-30$, $N=18$, $P=0.014$). 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 towards 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 mouthhold 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 range 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 towards novel females, the predicted trend would be a strong response towards females with the most conspicuous paint mark (e.g. on the neck, $N=5$), an intermediate response towards females with an inconspicuous paint mark (e.g. tip of the tail, $N=5$), and a weak response towards females with no paint mark ($N=4$). Only one of the six variables that measured male responses towards novel females (Table 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 towards females) assumes that: males are unable to differentiate among females; males may be able to differentiate between females, but show 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 towards the different classes of females.

The second hypothesis (H_2, males differentially respond towards 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 towards a male could enhance male reproductive success if the display rate indicates a greater chance of copulating with a female (i.e. that the 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 towards 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 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 towards reintroduced resident females that might indicate a social bond. In both our laboratory and field experiments males ignored resident females, while dramatically increasing courtship behaviour towards novel females. Furthermore, recent field studies of *A. carolinensis* describe a territory-based mating system of female-defence polygyny (Ruby 1984; Jenssen & 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 two to six females.

The last hypothesis (H_4, males differentially respond towards 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 with 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 travelled 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 towards novel females more frequently than towards 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 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 features unique to each resident female. These 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 towards 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 defence, 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 4). The magnitude of redirected social activities indicate the extent to which males reapportion their attention and priorities towards 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 towards 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 norepinephrine (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 signalling 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 centimetres apart. Thus, separation distance is not an explanation for diminished head amplitude during signalling. 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 nonresident 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 displayed 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* showed 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 to the view 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 favour 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 nonreceptive 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 males 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 towards chemical stimuli of novel females than towards familar females (*Eumeces laticeps*, Cooper 1996; *Eublepharis macularius*, Steele & 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 & Shine 1998), where males form long-term pair bonds with single females, presumably as a form of mate guarding. Neighbour recognition (i.e. dear enemy phenomenon, sensu Temeles 1994) has been reported in *A. carolinensis* (Quaills & 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, by 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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