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Female mate choice in the non-territorial lizard *Ameiva plei* (Teiidae)

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Abstract Mate choice by females has been documented in a variety of taxa. Female mate choice in species lacking male resource control or paternal care might occur if preferred males provide protection from harassment. Female mate choice was investigated in a natural population of the non-territorial lizard *Ameiva plei* (Teiidae). Consort pairs were allowed to form naturally. Consort males were significantly larger than non-consort males. After removal of consort males, the "abandoned" female's reaction to the first male who approached her was recorded. Females rejected all small males. Female preference for large males was significantly higher than preference for small males. Large males may be better equipped to guard the females from harassment and behavior of large males is less harassing than behavior of small males, thereby affording the female increased foraging time.

Key words Female choice · *Ameiva plei* · male size

Introduction

A recent review of mate choice in lizards (Tokarz 1995) noted that whereas there is now much evidence that female choice occurs in fishes, amphibians and birds, there is much less evidence for female choice in reptiles. The shortage of mate choice studies on reptiles is peculiar in that some reptiles, in particular lizards, seem to be ideal candidates for investigating mate choice. Lizards often exhibit sexually dimorphic coloration and conspicuous behavioral displays, providing obvious phenotypic characters on which mate choice might be based. In addition, lizards often have polygynous mating systems, leading to substantial variation in mating success among males that can be used to measure female preferences.

Most of the studies on female choice in lizards have focused on territorial species. It is thought that females of territorial species may have little opportunity to assess and compare different males because males tend to arrange their territories to enclose the female's territory, and males exclude other males from those territories. Therefore females rarely see more than one male at a time (Stamps 1983). Most studies have shown, in fact, that females choose mates based on the resources that the males defend and not on the physical attributes of males (Keister 1979; Ruby 1981, 1984; Trillmich 1983; Stamps 1987a,b; Hews 1990). In non-territorial species, however, females have the opportunity to encounter many males within a day (Anderson and Vitt 1990; Censky 1995a, 1996). Interestingly, the only study that has demonstrated female choice based on male attributes, namely body size, was that of a non-territorial species, *Eumeces laticeps* (Cooper and Vitt 1993). The few studies that have looked at sexual size dimorphism in non-territorial lizards (Anderson and Vitt 1990; Censky 1995a, 1996) have demonstrated that sexual selection occurs due to large male advantage in intrasexual encounters. Female choice, however, has not been explored in these species.

In his review, Tokarz (1995) called for more studies to test whether mate choice occurs in lizards, and suggested that species that have "some special aspect of their ecology..." would be appropriate. Tokarz recommends *Anolis valencienni* because, unlike other *Anolis* which are territorial, sit-and-wait foragers, *A. valencienni* is a non-territorial, active forager. Therefore, females in this species have the opportunity to encounter many males while foraging. I suggest, like Tokarz, that non-territorial lizards may provide an opportunity to examine non-resource based female choice. Instead of focusing on a species whose non-territorial spacing system is the exception in its family, I have investigated a species for which non-territoriality is the norm among its relatives.

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If female choice is found in "non-territorial" species in general, evolving multiple times in independent lineages, this may prove to be more convincing evidence of adaptation.

Ameiva plei is a non-territorial teiid lizard which is sexually dimorphic in size, with males attaining larger body sizes than females. Both males and females spend a large portion of the day foraging within their home ranges, and home ranges of both sexes overlap extensively (Censky 1995a). Therefore, females have ample opportunity to assess the phenotypic quality of different males. There is strong evidence that intrasexual competition for access to mates has favored large body size in males of this species (Censky 1995a, 1996). A demonstration that male body size is influenced by intraspecific competition, however, does not preclude mate choice by females also influencing body size. While both forms of sexual selection are often discussed as separate entities with no influence on the other, both components may be operating in many mating systems (Cox and Le Boeuf 1977; Searcy 1982; Partridge and Halliday 1984; Bradbury and Davies 1987; Catchpole 1987). Large body size is strongly associated with dominance in interactions between males in many species (Dugan 1982; Dugan and Wiewandt 1982; Pratt et al. 1992; Rodda 1992; Cooper and Vitt 1993; Censky 1995a). Female choice of mates, however, could reinforce selection for exaggerated traits, such as large body size of males (Searcy 1982). Of course, for mate choice to result in sexual selection it must affect reproductive success differentially (Searcy and Andersson 1986).

In this paper, I present data on field experiments to determine whether female mate choice occurs in *Ameiva plei*. The hypothesis tested was that mate choice by females was influenced by the body size of males. More explicitly, I investigated whether females show a preference for the largest males among those they encounter. If females exercise choice, they would be expected to reject small males that they encounter.

Materials and methods

The study was conducted between 21 June and 25 July 1995 on the island of Anguilla, northern Lesser Antilles. The study site was described in Censky (1995a). Lizards were captured by noosing. A series of four colored beads was sewn onto the base of the tail to permit individual identification. Lizards were measured for snout-vent length (SVL; nearest 1 mm) and weighed (nearest 1 g) and released at the site of capture.

Females in this population are not synchronous in their receptivity (Censky 1995a). Therefore, in order to test a sufficient number of females in the choice experiments, both naturally receptive and females of induced receptivity were used. To induce receptivity, females were injected subcutaneously with estradiol. I modified the protocol for inducing receptivity established by Cooper et al. (1986) as follows: females were injected with 1.0 µg 17-β estradiol in 20 µl safflower oil each day for 4 days. Induced females were held in cages and supplied with food for the period of injections. They were then released at the site of capture. Ideally, naturally receptive females also should have been held in captivity to reduce any effects of captivity between naturally receptive and induced females; however, this could not be done because receptivity in this population lasts for only 2–4 days (Censky 1995a), allowing insufficient time for both captivity (for 4 days) of naturally receptive females and experimental runs of those females. Twelve females were induced to receptivity and three females were found naturally receptive.

Induced females were released late in the day. After release, these females typically disappeared quickly into their burrows. The following day, I allowed male-female pairs to form naturally. On the first day of receptivity, males typically fight over females, with the largest male attaining the "right" to guard the female (Censky 1995a). The male guards the female, staying in close proximity to the female for the entire day. Just before the female retreats to her burrow, the male usually copulates with her; she then retreats and the male often covers her burrow and guards it for up to 30 min. He then retreats to his burrow. The next day the guarding male is waiting at the female's burrow when she emerges and another day of guarding begins. The male guards the female for the duration of her receptive period and usually mates with her just prior to and just after his absences from her (i.e., when she is in her burrow) (Censky 1995a).

When a male guards a female and she subsequently mates with him, it is not clear whether the female actually prefers that male, or whether she has no choice but to mate with him because he keeps all other males away. The basic plan for my experiment was to provide a situation in which a female might exercise choice, as determined by either acceptance (= copulation) or rejection of a male. This was done by removing the guarding male, and then observing the female's reaction to other males that attempt to mate. The prediction is that if females exercise choice for large males, they will prefer the largest of available males.

In this experiment, half of the males were allowed to copulate and after the consort female retreated to her burrow, the male was collected. The other half of the males were collected prior to mating but just before the female retreated into her burrow. All males were held overnight. This was done to determine whether copulation would influence future female choice. The next morning, all interactions that occurred when the "abandoned" female emerged from her burrow were recorded. Females were followed for the rest of the day.

In 8 of 15 cases, the original consort males that had been held overnight were released near the female 2 h after she emerged from her burrow. The female's reaction was recorded along with interactions with other males.

Statistical analyses were done using Statmost 2.50 (Datamost Corp., Salt Lake City, Utah). The *t*-test was used to determine if SVL differed between consort and non-consort males. The Mann Whitney *U*-test was used when data did not meet assumptions for normal data. "Repeated measures" chi square (Linton and Gallo 1973) was used to determine whether prior copulation influenced future copulation by females. The null hypothesis was that there was no association between the two events. For all tests, level of significance is $\alpha \leq 0.05$.

Results

A total of 15 females was tested. Males who formed pairs with these females on the first day after the female's release (i.e., receptivity) were considered consort males. Non-consort males, on the other hand, were adult males that were within 10 m of females on the first day of receptivity, but did not pair with the female. Consort males had a mean SVL ± SD of 154 mm ±8.8 (140–165, $n = 15$) and non-consort males had a mean SVL ± SD of 97 ±17.37 (4–144; $n = 28$; Fig. 1). Consort males were significantly larger than non-consort males

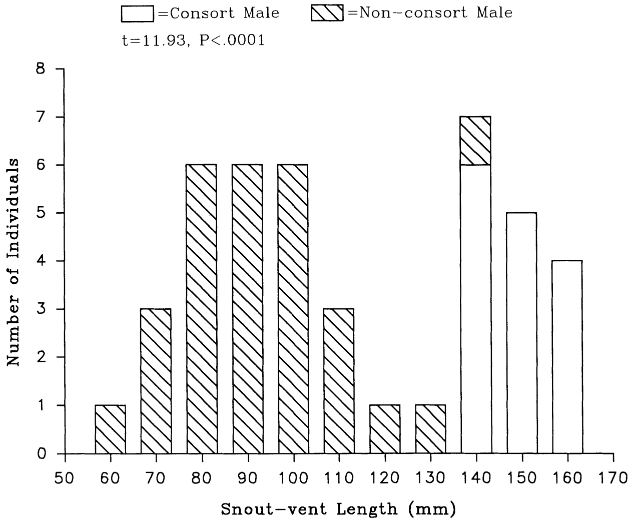

Fig. 1 Size distribution of consort males and non-consort males

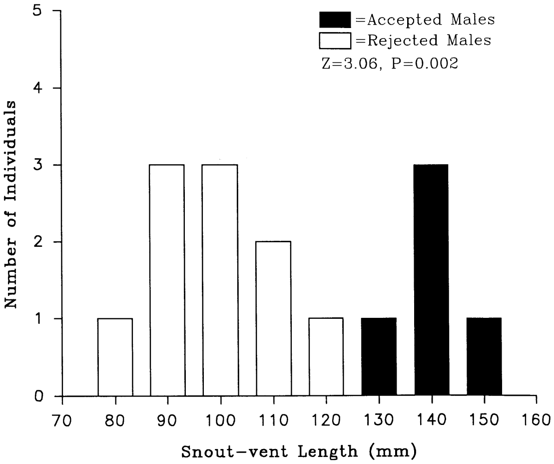

Fig. 2 Size distribution of males that were accepted by females and males that were rejected by females

($t_{(15,28)} = 11.93$, $P < 0.0001$). The males that formed consort pairs with naturally receptive females were not significantly different in size from those males that formed pairs with induced females (Mann-Whitney *U*-test: $Z_{(3,12)} = 0.144$, $P = 0.89$).

Each receptive female's reaction to the first "new" male that approached the morning after the initial male was removed was recorded. Of the 15 males that first approached the "abandoned" females 10 were clearly rejected. Females that had copulated with the initial male the previous day were not more likely to accept or reject other males ("repeated measures" $\chi^2 = 0.138$, $P > 0.05$). Females rejected males by either chasing them, nipping them, or running away. Males that were rejected pursued females for an average of 20.6 min (SD= 11.36, 8–44 minutes, $n = 10$). In no instance did the female that rejected the male later accept him. Males that were rejected ($\bar{x} = 101.5$ mm, $n = 10$) were significantly smaller than males that were not rejected ($\bar{x} = 144.2$ mm, $n = 5$; Mann-Whitney *U*-test: $Z = 3.06$, $P = 0.002$; Fig. 2).

Interestingly, the manner in which a small male approached a female differed from that of a large male. Small males always approached from the rear and immediately tried to mount the female. When the female moved, the small male persisted in trying to mount the female. A large male, on the other hand, approached the female from the front, slowly moving around to the tail, then moving his head anteriorly along the tail. If the female moved away, the large male would not persist. He would stay near the female, but he would not attempt to mount the female. The behavior of the large male may be related to experience and hence age of the individual.

Half of the males that were rejected were larger than the rejecting females, 3–12 mm larger (Fig. 3). However, rejected males were 10–43 mm smaller than the smallest (130 mm) accepted male. The difference between the smallest accepted male and the largest female was 15 mm (130 mm and 115 mm, respectively).

In 8 of 15 cases where the original consort male was released 2 h after the female's emergence from her burrow, all males found the consort females and began guarding them. In those instances where the female was being guarded by another male (4 of 8), the original male displaced the guarding male. In all cases the original male was larger than the displaced male.

Discussion

A number of studies suggest that in those species of lizards in which males do not provide females with resources, females mate with larger, more dominant males (Dugan 1982; Anderson and Vitt 1990; Rodda 1992; Censky 1995a). However, the only experimental evidence that female choice of mate is based solely on large body size was that reported for *Eumeces laticeps* (Cooper and Vitt 1993). In that experiment, females overwhelmingly demonstrated receptivity to large males and refusal to mate with small males even in the absence of large males.

Like *Eumeces laticeps*, female *A. plei* appear to choose large males as mates. In this population, females clearly rejected small males and accepted large males. In addition to rejecting males shorter than themselves, *A. plei* females rejected males that were as much as 12 mm longer in SVL (i.e., females accepted only the largest males).

Although females chose large males as mates, it was unclear whether female choice was based on male body size or on age/experience, as body size up to a certain size is correlated with age in this population (Censky 1996). It has been suggested that female preference for

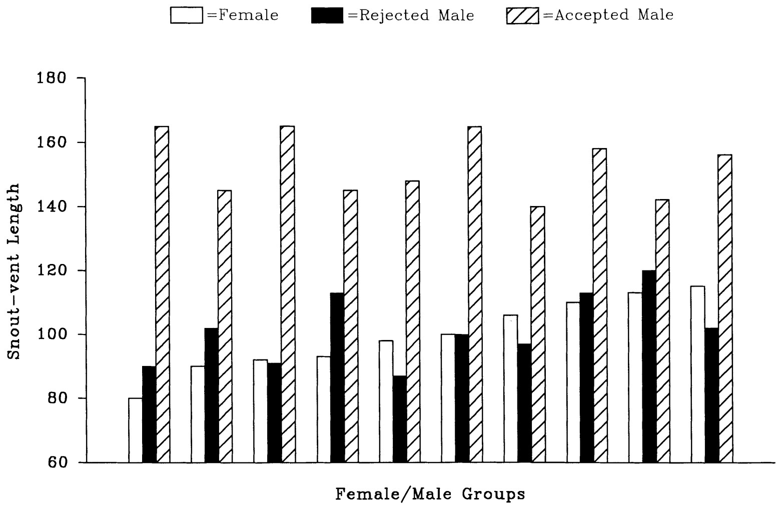

Fig. 3 Females grouped with the male that they rejected and the male that they accepted, by size

older rather than larger males may be common in species with indeterminate growth (Coté and Hunte 1993). Age reflects not only survival ability, but also may indicate quality genes for the offspring (Halliday 1983). A female that mates with a vigorous male (e.g., a male that has survived well into adulthood) may gain an evolutionary advantage by passing those genes on to her offspring (Kirkpatrick and Ryan 1991). Female preference for males possessing genes for high viability arises indirectly, through selection favoring a trait genetically correlated with the preference rather than favoring the preference directly. Indirect selection is expected to occur in species that form leks (Dugan 1982; Rodda 1992) or are non-territorial (Cooper and Vitt 1993). Direct selection, on the other hand, occurs when the choice the female makes affects her survival and fecundity. Direct selection has been implicated in most studies of female choice in lizards. Females choose males based on the quality of the resource (e.g., territory) that the male holds (Trivers 1976; Andrews 1985; Hews 1990; Pratt et al. 1992) and these resources affect the female's survival or fecundity.

A. plei is a non-territorial species of lizard, and as such it is often assumed that males control few if any resources. Therefore, female choice should be attributed to indirect selection. It is possible, however, that *A. plei* males do have a resource to offer females, namely increased foraging time. Females in this population spend significantly more time foraging when they are being guarded than when they are alone (Censky 1995a). Males, however, spend significantly less time foraging while guarding. This is primarily because the guarding male remains alert to all activity while guarding the female. He stations himself near the female, sometimes touching her. While guarding, the male chases away all other males. In addition, he may alert the female to potential predators by his sudden jerky movements (E. Censky, personal observations). Female activity while being guarded is primarily foraging (67.9%) (Censky 1995a). By focusing attention solely on the male that is positioned near her, instead of having to survey the 360° world around her, the female may be afforded increased time for foraging.

A small male may be ill-equipped to guard a female and defend her from harassment from other males. Thus, her foraging time would be decreased due to increased mating attempts from other males. In addition, the behavior of a small male when attempting to mate with a female could be termed persistent, if not harassing, behavior. Small males tend to continue trying to mount females even though they have been rejected, whereas large males, once rejected, will retreat to guarding behavior and not attempt to mount the female until much later. It has been shown in some species of fish that females choose large males to avoid harassment from small males (Warner and Hoffman 1980; Van den Berghe et al. 1989). Increased foraging for a female should be reflected in both female survival and fecundity, as the more food a female takes in, the larger she grows. Larger females have larger clutches and more clutches in a season (Censky 1995a,b).

My data suggest that female *A. plei* show a preference for large males, rejecting males that are not at least 130 mm in size. Males offer no tangible resource, and superficially it appears that females are choosing large males based on the male quality reflecting superior genes (indirect selection). Females, however, actually may be selecting large males based on both size and experience. Their superior ability to "guard" and their low level of copulatory harassment may increase the time that females can spend foraging, thereby increasing the female's lifetime reproductive success.

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