Behavioural Processes 83 (2010) 282–286

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Social influences on female choice in green anole lizards (*Anolis carolinensis*)

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ARTICLE INFO

Article history:
Received 9 July 2009
Received in revised form
13 November 2009
Accepted 11 January 2010

Keywords:
Green anole
Mate choice
Social influences

ABSTRACT

We conducted an experiment on female *Anolis carolinensis* lizards to investigate whether social factors influenced their selection of an end-chamber in a test arena. We tested (1) whether characteristics of males previously seen in the end-chambers would influence female choice and (2) whether the presence of other females simultaneously choosing would influence choice. In experiment one, females observed a large and a small male in the end-chambers prior to choosing. Females were tested individually and in pairs. When tested individually, females preferred the end-chamber previously inhabited by the larger male. When females were tested in pairs, however, in each case one female chose the large male's end-chamber and the other female failed to make a choice. In experiment two, we conducted the same paired-choice test, but prior to the test we evaluated the dominance relationships between the pair of females. In the majority of cases, the more dominant female was the one to enter the large male's end-chamber. Results indicate that females are influenced by the presence and characteristics of males, but that female competition also plays a role in choice.

1. Introduction

In many species, social interactions can influence female dispersal, territory selection, mate choice, and even mating systems. Most commonly, male–male interactions are studied to understand territory settlement, and female–male interactions are studied to understand assortative mating (Bateson, 1983; Andersson, 1994). It is becoming clear, however, that interactions among females can be important for mate selection. For example, females can use social information acquired from observing other females to modify their mate preferences and their mate choices (Westneat et al., 2000; White, 2004). Female competition can also play a role in influencing other females' mate choices. If female competition affects assortative mating, then ignoring it may serve to obscure our understanding of mate choice and mating systems.

Research in lizards has provided inconclusive results as to what information females use when selecting home ranges and mates (Stamps, 1983; Olsson and Madsen, 1995; Tokarz, 1995). It is possible that for species with no parental care, there are few benefits to be gained as a consequence of being choosy when selecting a mate. Instead, resources other than the quality of the male (such as food or shelter) may be more important for successful reproduction. Alternatively there could be direct and indirect benefits resulting in being choosy about mates, even for non-parental reptiles. Males can vary in their resource holding potential and thus selecting a dominant male could provide priority access to quality resources. In addition, heritable attributes of males such as body size, dewlap coloration, or bite force have been shown to be indicators of growth rates, ability to capture prey, ability to maintain a territory, and dominance (Tokarz, 1995; Lailvaux et al., 2004). Thus selecting mates based on these characteristics could result in the production of higher quality offspring (Andersson, 1994). Some recent evidence does support the possibility that females in many lizard species are choosy when selecting mates and they may gain indirect benefits as a consequence (Olsson et al., 2003: Hamilton and Sullivan, 2005; Sullivan and Kwiatkowski, 2007; Lancaster et al., 2009).

The literature on the mating patterns of green anoles (*Anolis carolinensis*) provides confounding reports of what information, if any, is used by females to choose mates. In early work, green anoles were considered to have a protandry-based mating system (Crews, 1975). In such a model, similar to a polygyny threshold model (Orians, 1969), males establish territories around resources that are important for female fitness and actively exclude other males from these territories. Females then select among the males' territories based on the quality of resources available, the quality of the resident males, and the number of other females present.

Data from field studies have led to a reevaluation of the green anole mating system altogether. Jenssen et al. (2001) revealed that there was no sex-related difference in when anoles emerge from hibernacula. This suggests that females are selecting locations to breed at the same time males are beginning to establish territories. This timing would not allow females to be able to assess resident males prior to mate choice, and breeding area selection (but see

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0376-6357/$ – see front matter
doi:10.1016/j.beproc.2010.01.005

Calsbeek and Sinervo, 2002a). Jenssen et al. (2001) suggested that females mate with males that reside in areas abundant in resources. Therefore sexual selection may act on the ability of males to hold the best territories, while female choice for male characteristics plays no role in selection of a breeding area (Lightbody and Weatherhead, 1988; Nunez et al., 1997). In support for such models, laboratory research has failed to find female preferences for indicators of male quality (MacDonald and Echternacht, 1991; Lailvaux and Irschick, 2006).

If females are selecting breeding areas prior to males engaging in competition or courtship, then females would have little opportunity to evaluate many aspects of males' competitive behaviour. Male body size however, could be a trait that females could observe and evaluate at any time. Body size can be an honest indicator of male age, fighting ability, and health (Tokarz, 1995; Jenssen et al., 2000). Females show trends to prefer larger males across a variety of lizard species (Dugan, 1982; Cooper and Vitt, 1990). Results from laboratory and field studies of green anoles, however, provide contradictory reports on whether female preferences for male body size are important for mate selection (Andrews, 1985; MacDonald and Echternacht, 1991; Jenssen and Nunez, 1998).

It is possible that laboratory studies in confined conditions do not accurately test female mate preferences, as females may not approach large, aggressive males in restricted areas even if they have a preference to mate with the males. By contrast, in the field it is often impossible to control the numerous confounding variables that might influence the relationship between mate preference and mate choice (Jennions and Petrie, 1997). For example, female mate choice may be influenced by the presence of other females in ways that could obscure the role mating preferences may play on mate selection.

There has been little research on the importance of interactions among females in green anoles. Female do not hold and defend territories like males do, and their home ranges overlap (Nunez et al., 1997). Females do show some intrasexual aggression, although much less than males (Andrews and Summers, 1996). Resident females display to and pursue females who intrude into their home ranges (Evans, 1936). Andrews and Summers (1996) found that when females were paired in cages, dominance hierarchies developed. Female aggression was most often directed by dominant females toward subordinates in an effort to prevent subordinates from interacting with males. Dominant females exhibited more aggressive behaviour than subordinates. With the introduction of a male into the cage, dominant females also courted males more than did subordinate females.

We examined whether females would show any sensitivity to the characteristics of resident male anoles when selecting an end-chamber in a testing arena, and also whether the presence of other females would influence that choice. In two experiments, we provided females with the opportunity to choose between two end-chambers. The only difference between the two end-chambers was that females could observe a small male in one of the end-chambers and a large male in the other prior to the time of choice. Females were allowed to enter the end-chambers after the males were no longer present, thus while this was a laboratory test and females were selecting end-chambers that were much smaller than actual home ranges in the wild, we did not force females to interact with males in confined quarters. Females were randomly assigned to pairs and then tested twice; once singly and once simultaneously with the other female. We had two goals; first, to determine whether females would use characteristics of the previously observed males when selecting an end-chamber. We hypothesized that larger males would be preferred to smaller males and this preference would dictate females' selection of end-chamber. Second, we attempted to determine whether intrasexual factors could modify female choices. Given results of Andrews and Summers (1996), we hypothesized that dominance relationships among females would play a role in influencing end-chamber selection and that dominant females would get priority choice.

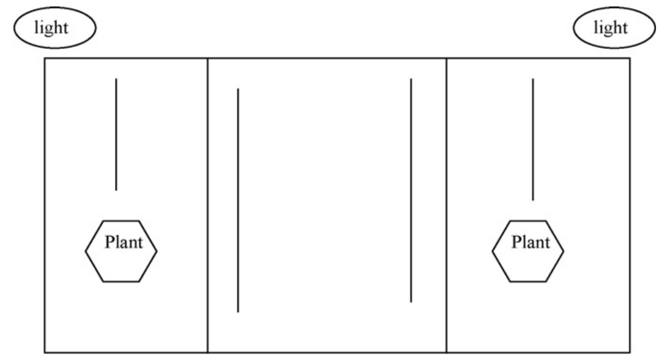

Fig. 1. Scale schematic of area choice apparatus. Females began the test in the middle area and could see a small and large male in the end-chambers (sides counterbalanced across trials). Lines indicate wooden perches. Perches in middle chamber ran horizontal at the wire partition, perches in end-chambers ran diagonally toward light source. Water was dripped onto plants in end-chambers.

2. Experiment 1

2.1. Materials and methods

We purchased 24 females (weighing between 2.05 and 3.81 g), four large males (weighing between 5.94 and 5.87 g), and four small males (weighing between 3.51 and 2.98 g) from Carolina Biological Supply. All anoles were originally wild caught in South Carolina in May through June. Upon arrival to our laboratory, we placed dots of coloured, non-toxic water-based paint on the back of each anole to permit individual identification. We housed females together in a 60 cm × 120 cm × 30 cm holding cage for 7 days prior to the commencement of testing. We housed all males together in a 90 cm × 45 cm × 40 cm cage, but it became apparent that the larger males were so much more aggressive than the smaller males that 2 days before commencing the experiment we removed the large males and housed them individually in 60 cm × 45 cm × 30 cm cages. All cages contained wood mulch substrate and rocks, plants, and branches. We dripped water into each cage constantly. We maintained all lizards on a 14:10 h light:dark schedule using both ambient light and directional light from 100 W full-spectrum bulbs directed over one corner of each cage. Room temperature ranged from 27 to 30 °C during light and was approximately 26 °C at dark. The long light cycle and warm conditions simulated breeding season conditions. We gave all anoles *ad lib* access to mealworms, and supplemented the diet with calcium-dusted crickets. We selected the 14 largest females from the 24 purchased to be subjects in the experiment. We house the other 10 females with two males that were not used in the main experiment. These extra anoles courted, mated, and produced offspring, suggesting that our subjects were in breeding condition.

One day before the trial, we randomly selected a pair of females and moved them into a 45 cm × 45 cm × 40 cm holding cage where they remained for 24 h. The test occurred in a 90 cm × 45 cm × 40 cm cage with two 6 mm-grid hardware cloth dividers separating the cage into two 45 cm × 40 cm × 27 cm end-chambers and one 45 cm × 40 cm × 36 cm middle chamber (Fig. 1). We cut a 2.5 cm hole in the hardware cloth 15 cm from the front and 12 cm from the bottom of the cage and covered it with a fitted piece of white paper. The two end-chambers each contained one plant, a large branch, food, water and each had a light source directly above it. The middle chamber only contained two branches, each one approximately 5 cm from each of the dividers. All cham-