AGGRESSION, AND THE ACQUISITION AND FUNCTION OF SOCIAL DOMINANCE IN FEMALE ANOLIS CAROLINENSIS

by

THOMAS J. ANDREWS and CLIFF H. SUMMERS[1,2)]
(Department of Biology, University of South Dakota, Vermillion, SD 57069, USA)

(Acc. 28-V-1996)

Summary

Female green anoles, *Anolis carolinensis*, were paired in terraria to investigate behavioral components of social interaction. Resources (perching sites, prey, and males as potential mates) were limited to assess their importance to cohabiting females. During interaction, paired females exhibited aggressive social behavior which contributed to the development of dominant-subordinate relationships. Dominant status and its relationship to differential resource acquisition was defined primarily by frequency of displacement of another female. Along with displacement, dominant females also had increased frequency of assertion displays, challenge displays, attacks and biting (Figs 1 & 2). Subordinate females were displaced more often and assumed submissive postures. No differences were found between dominant and subordinate females for perch site selection, body color or in prey capturing latency or success (Figs 3 & 4). Perch site elevation was not different between dominant and subordinate females, but was significantly lower than males. The color of paired females was not different unless males were present, in which case dominant females were darker. Paired females also respond differently to courtship display (Fig. 5). Dominant females responded with displays significantly more often than subordinate females to male courtship, indicating receptivity. The role of dominant-subordinate relationships among female *A. carolinensis* may include courtship and reproductive success as an important component, with consequences for the outcome of aggressive and reproductive social interactions with males.

[1)] Corresponding author; e-mail: Cliff@Charlie.USD.EDU

[2)] We would like to thank B. Graves, N. Greenberg, A. Johnson, T.A. Jenssen, J.M. Matter, K. Orrell, K.J. Renner, T.R. Summers, D. Swanson and G.R. Ten Eyck for constructive criticisms on the manuscript. This research was supported by NSF grant #OSR 9108773.

Introduction

Many lizard species are known to manifest social dominance relationships in natural settings and when placed in laboratory enclosures, where crowding may result in increased social interaction, increased aggression, and a switch to hierarchical behavior (Carpenter, 1960, 1961; Brattstrom, 1974). Formation and maintenance of density-dependent dominance hierarchies is the result of species-specific aggressive behavior, and has been observed in *Sceloporus undulatus* (Carpenter, 1962), *Cnemidophorus sexlineatus* (Brackin, 1978; Carpenter, 1960, 1962), *Dipsosaurus dorsalis* (Carpenter & Grubitz, 1960), *Amphibolurus barbatus* and *Ctenosaura hemilopha* (Brattstrom, 1971, 1974) and in a parthenogenetic lizard, *Cnemidophorus uniparens* (Grassman & Crews, 1987).

Aggressive behavior and formation of dominance hierarchies in the genus *Anolis* has been observed in *A. aeneus* (Stamps, 1976; Stamps & Barlow, 1973; Stamps & Crews, 1976), *A. nebulosus* (Jenssen, 1970), *A. sagrei* (Evans, 1938; Tokarz, 1987, 1995), *A. townsendi* (Carpenter, 1965), and *A. carolinensis* (Evans, 1935, 1936a; Greenberg & Noble, 1944; Mason & Adkins, 1976; Greenberg *et al.*, 1984; Greenberg & Crews, 1990). Displays, which include aggressive behavior, play an important role in the establishment of dominance (described for *Anolis carolinensis* by Greenberg & Noble, 1944; Crews, 1975; Greenberg, 1977; DeCourcy & Jenssen, 1994) and characteristically occur in four contexts: 1) assertion, 2) challenge, 3) courtship, and 4) submissive behavior by subordinate individuals (Greenberg, 1977).

Among males, most of the difference between individuals having won or lost aggressive interactions has been attributable to body color, perch site selection, and circulating androgen (Greenberg & Crews, 1990). During agonistic encounters, the first of two lizards to display a postorbital eyespot was the eventual winner 93% of the time (Summers & Greenberg, 1994), and then subordinate males were darker in color (more brown) than dominants (more green), occupied lower perch sites, and had depressed rates of courtship relative to winners of fights (Greenberg & Crews, 1990; Greenberg *et al.*, 1984).

Aggressive behavior and reproductive physiology of male and female *A. carolinensis* are intrinsically concatenated (Crews & Greenberg, 1981). Intruding females initially elicit displays of assertion from territorial males.

Females avoid males or respond by performing characteristically submissive displays, which frequently initiate courting behavior (Crews & Greenberg, 1981). Courtship facilitates the stimulatory effects of environment and is necessary for normal pituitary gonadotropin secretion (Crews, 1974, 1975). Alternatively, female observation of male-male aggressive behavior has been shown to inhibit environmental stimulation of ovarian growth (Crews, 1974). Thus, the context of display behavior appears to be important to the physiological and behavioral development of female *A. carolinensis*.

Observed social systems of female *A. aeneus* ranged from territoriality in some habitats, to dominance hierarchies in others, independent of population density (Stamps, 1973). Female *A. sagrei* have also been observed to be territorial against non-resident females (Evans, 1938). Aggressive display behavior is similar in male and female *A. carolinensis* (Greenberg & Noble, 1944), and is displayed by females toward nonresident females introduced into their territories (Evans, 1936b). Resident females defeat nonresident females in most encounters, and the resident is usually the only overtly aggressive individual (Evans, 1936b). In a semi-natural population of male and female *A. carolinensis*, females dominated other females through aggressive behavior and display (Greenberg & Noble, 1944). During courtship and mating, dominant resident females in a male's territory consistently drove out intruding females or forced them to hide, resulting in diminished opportunities for mating behavior. However, a dominant female is more likely than a male to tolerate others and does not usually succeed in keeping a female intruder out of the territory for very long (Greenberg & Noble, 1944).

It was the purpose of this study to quantify social dominance among females, and to compare its functional value with dominant/subordinate male-male interactions. We hypothesized that one female of a pair would more often physically displace a cohabiting female during social interaction and exhibit a greater frequency of aggressive behavior. That is, it was hypothesized that female *A. carolinensis* will develop social relationships based on hierarchical or dominant/subordinate status when social interactions are limited to a pair of females.

A possible behavioral result of dominant status in females is a priority of access to important resources, as is true for male-male interactions.

Dominant males consistently choose higher perch sites, have lighter body color, and have a higher frequency of courtship with greater courtship success than subordinate males (Greenberg & Crews, 1990). As food may be a limited resource, partitioned unequally, access to it may also be dependent on social interactions. Our hypotheses regarding resource utilization were that the dominant female will have (on average) a higher perch site, lighter color, will capture (with shorter latency) and eat prey more often, and be responsive to male courtship displays more often than the subordinate female.

Methods

Forty adult female and fifteen adult male *Anolis carolinensis* were obtained from a commercial supplier (Buck's Live Animals, La Place, LA). Each lizard was weighed, measured (snout-vent length), sexed, marked, housed individually in glass terraria (51 × 30 × 26 cm), and treated in accordance with conditions commensurate with the 'Principles of laboratory animal care' (NIH publication No. 85-23) and the USDACUC. There were no significant differences in mean initial weights and snout-vent lengths among dominant, subordinate or control female lizards, nor were there differences among males. Lizards had water *ad libitum* and were fed crickets every other day. The photoperiod was 14L : 10D, with temperatures of 32°C and 20°C during photophase and scotophase respectively (Licht, 1968, 1972), at a relative humidity of 80%. Lizards were allowed to acclimate to these conditions for a period of 10 days before experiments began. Individual females were marked for identification by unique combinations of alternating yellow and white bands, positioned on the last 1cm of their tails using non-toxic acrylic craft paint (avoiding the color red). Behavior was observed (visually and recorded on video tape) with the room darkened, except for lights immediately above the terraria. Each terrarium was partitioned by a removable opaque divider, and sides and rear glass were covered with opaque paint, inhibiting interaction between cages and leaving the front and top side of each terrarium clear for viewing and lighting purposes. Each side (one-half) of the terrarium contained a wooden perching stick (except as noted), a water dish, and a single female *A. carolinensis*.

Female response to another female

Female *A. carolinensis* were housed individually ($N = 10$; as control) or as pairs ($N = 30$ or 15 pair) on either side of the opaque divider. The experiment consisted of removing the opaque divider, exposing the opposite side of the tank to the resident female. Behavior was recorded for a period of ten minutes before the divider was pulled, and then immediately to three hours after the divider was pulled.

Displacement (from perch sites, other sites or food) and lowered posture (body flat with head down and legs back), characteristic of subordinate males (Greenberg & Crews, 1990), defined subordinate status in females for these experiments. Displacement occurred if one female moved to the position of another and physically, spatially supplanted that animal.

A dominant-subordinate pair was identified when one female was displaced significantly more often than the other. Only female pairs which showed dominant-subordinate relationships were used in statistical comparison of behavior.

The following behavior was specifically recorded: Number of displays (with accessory movements; Hover & Jenssen, 1976) typically used in assertion, challenge, and submissive contexts (hereafter simply designated as assertion, challenge and submissive displays), number of attacks and bites (fighting), number of times displaced, time spent on 'home' side, and time spent on novel side. The assertion display, most often performed by adult males, consists of a characteristic sequence of deep and shallow head nods which may be accentuated by pushups and a brief extension of the dewlap. A challenge display in *Anolis* includes an extended or engorged throat, sagittal expansion, lateral orientation to an antagonist, four-legged pushups, the erection of nuchal and dorsal crests along the neck and back (in males only), darkened postorbital eyespots, and if an encounter is not interrupted by the retreat of one of the antagonists, then jaw-sparring and lock-jaw (Greenberg, 1977). During repeat encounters, chases appear to be a means of reinforcing dominance (Carpenter, 1967).

Submissive displays and accessory behavior of subordinate animals typically include rhythmic head nods, lower posture with body flat, head down and legs back, and darker color. The common posture consists of pressing the body against the substrate, extending the legs to the side or backwards, and closing the eyes. Submissive action is successful in stopping intraspecific as well as interspecific aggression, decreasing the amount of attention (usually agonistic) received from a dominant individual, and reducing energy expenditure (Carpenter *et al.*, 1970; Brattstrom, 1971, 1974). Submissive posturing may also allow females and young males to remain within the territory of a dominant male lizard (Brattstrom, 1974).

Dominance behavior and access to food

Nine dominant-subordinate female pairs and nine single females (control) were used to determine differences in time to prey capture and which females were successful. A small glass petri dish containing a single cricket placed in the center of the terrarium, allowing each lizard equal access, was observed until the prey had been consumed or 10 minutes had elapsed. Crickets had hind legs and the tarsi of front and middle legs removed to eliminate escape, but allow movement to attract the resident female lizards. At the end of the observation period additional crickets were added to the terrarium to ensure all females fed. The procedure was conducted three times (on separate days, 2 days apart) for each female pair and single female.

Dominance behavior, color and access to perch site

Nine previously established dominant-subordinate female pairs were observed (for color and position) three times daily (11 am, 2 pm, and 5 pm) for five consecutive days on a clean perching stick placed in the center of the terrarium. Previously used perching sticks were removed. Color was based on a scoring protocol in which 1 = green, 2 = part green/part brown, 3 = light to moderate brown, and 4 = dark brown (see Summers & Greenberg, 1994). A similar type of scoring protocol was used for determining average perch position chosen: 1 = top of the perch, the favored environmental surveillance sight for males, 2 = upper half of perch, 3 = lower half of perch, 4 = on the substrate, 5 = covert perching (Summers & Greenberg, 1994).

Dominance behavior and access to a male

A single male *A. carolinensis* was placed in each terrarium with a dominant-subordinate female pair. Only sexually responsive females and males were used, as determined by repetitive courtship displays when introduced singly to an individual of the opposite sex prior to the experiment. The male-female encounter was allowed to last for 20 minutes, after which time the male was removed. During encounters the number of assertion and challenge displays by male and females, number of rapid headnods (characteristic of courtship) by male, and the number of headnods by females were recorded.

Statistical analyses

Dominant and subordinate female pairs were distinguished by binomial test (critical $\alpha < 0.05$) from those without a significant asymmetry of displacement. Comparisons were made statistically for aggressive, submissive and courtship behavior, perch site selection and color by paired *t*-test or ANOVA. Potential differences between dominant and subordinate females in number of prey eaten and time to capture were analyzed statistically by a binomial test and Wilcoxon matched-pairs test, respectively.

Results

Female response to another female

A significant ($p < 0.027$) majority of paired female *Anolis carolinensis* form dominant-subordinate relationships, as differences in frequency of displacement between individual females within a pair were significant in nine out of eleven pairs. Females which were displaced significantly more often ($t_{16} = 9.6$, $p < 0.001$; Fig. 1) were designated as subordinate females. Two female pairs exhibited low frequency of displacement during social encounters and were not used in subsequent analyses.

Among paired female *Anolis* with defined social status, aggressive behavior in the form of assertion ($t_{16} = 5.09$, $p < 0.001$) and challenge ($t_{16} = 1.9$, $p < 0.05$) displays, was found to occur significantly more often among dominant females (Fig. 1). The number of attacks ($t_{16} = 3.6$, $p < 0.005$) and bites ($t_{16} = 3.14$, $p < 0.01$) by dominant females were also significantly higher (Fig. 2). Submissive postures were seen significantly ($t_{16} = 3.6$, $p < 0.001$) less often among dominant females than subordinate females (Fig. 2). Control females did not show any aggressive or submissive behavioral displays.

There were no significant differences in the amount of time spent on the novel side of the cage between paired and control females during the

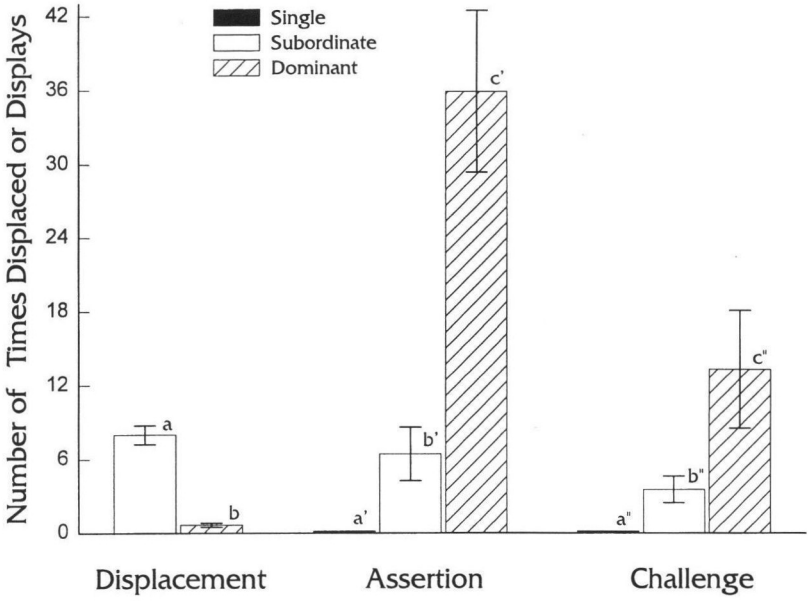

Fig. 1. Mean (± SEM) number of times displaced, or number of assertion and challenge displays by dominant, subordinate, and single females. Displacement, assertion and challenge displays were never observed in single females. $N = 9$ or 10 for all groups. Significant differences are indicated by differing letters (superscript a is significantly different from b and c, and b is different from a and c) just above the mean.

10 minutes after the divider was pulled ($t_{16} = 0.29$, $p < 0.389$), or three hours after the divider was pulled ($t_{16} = 0.98$, $p < 0.176$). For the remaining experiments both females of a pair had access to the entire enclosure.

Dominance behavior and access to food

The number of crickets captured and eaten by dominant and subordinate females was not significantly different (binomial test, $N = 18$, $p > 0.25$). Females were also similar in the amount of time it took them to capture their prey (Fig. 3), as dominant females were not significantly quicker in securing prey ($t_{18} = 5.0$, $p > 0.05$). When comparing the average time taken to capture the prey item between isolated and paired females, a significant difference was found in only one out of three feeding trials. Paired females had a significantly shorter capture time in trial 1 ($t_{18} = 2.58$,

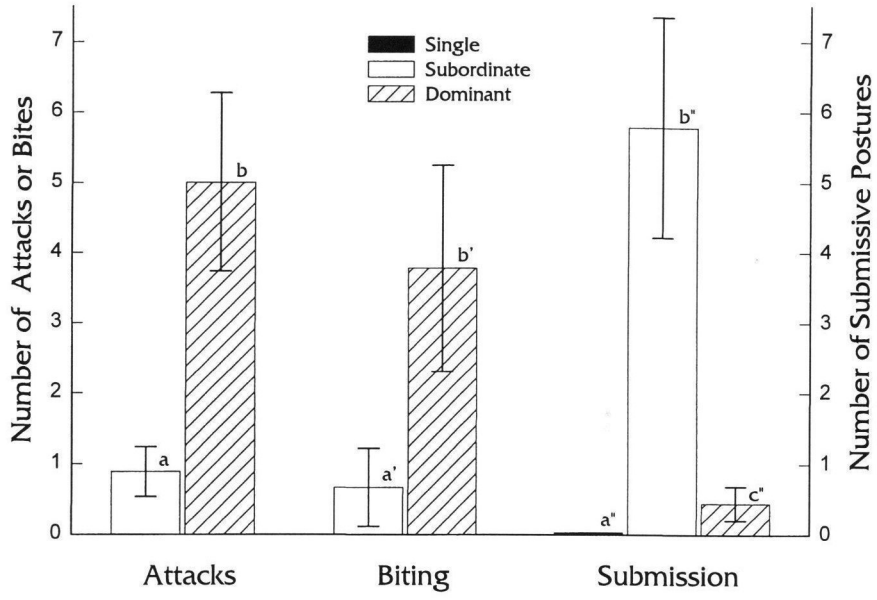

Fig. 2. Mean (± SEM) number of attacks and bites or submissive behaviors by dominant, subordinate, and single females. Submissive behaviour, attacks or biting were never observed in single females. $N = 9$ or 10 for all groups. Significant differences are indicated by differing letters (superscript a is significantly different from b and c, and b is different from a and c) just above the mean.

$p < 0.02$). There was no significant difference between paired and single females in trials 2 and 3.

Dominance behavior, perch site and color

Perch site selection was not significantly different between dominant and subordinate females ($t_{16} = 0.42$, $p > 0.68$; Fig. 4). On average, both female groups were positioned on the lower half of the perch.

Dominant and subordinate females were also not significantly ($t_{16} = 1.92$, $p > 0.072$) different in mean body color in the absence of a male; all visible pigmented body surface of both females were a light to moderate green (Fig. 4). However, when males were present body coloration was significantly darker in all females, and statistically darkest in dominant or single females ($F_{5,53} = 16.393$, $p < 0.001$).

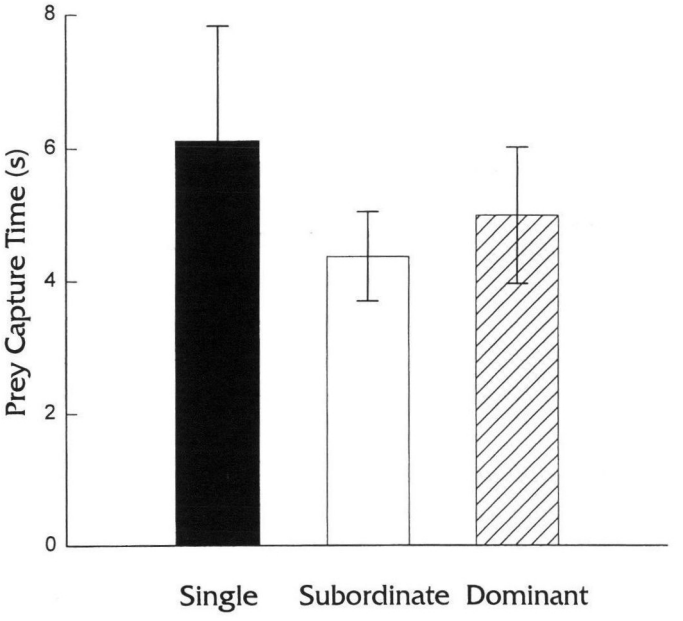

Fig. 3. Mean (± SEM) prey capturing time (s) of dominant and subordinate females. $N = 9$ for both groups. There were no significant differences among groups averaged over all trials.

Dominance behavior and responsiveness to a male

In response to male courtship displays, both females responded in all but two dominant-subordinate pairs. Within these two female pairs, the subordinate female in each case did not respond. Dominant females head nodded significantly more often than subordinate females ($t_{16} = 2.54$, $p < 0.02$) in response to male courtship displays (Fig. 5).

Discussion

When two female *Anolis carolinensis* were placed on opposite sides of a divided enclosure and subsequently allowed to interact, social behavior was evident. Females behaved differently in the presence of another female and exhibited increased frequency of social interaction (such as assertion, challenge, submissive displays, and fighting), which indicates that, under these conditions, females intensively interact and establish dominant-subordinate

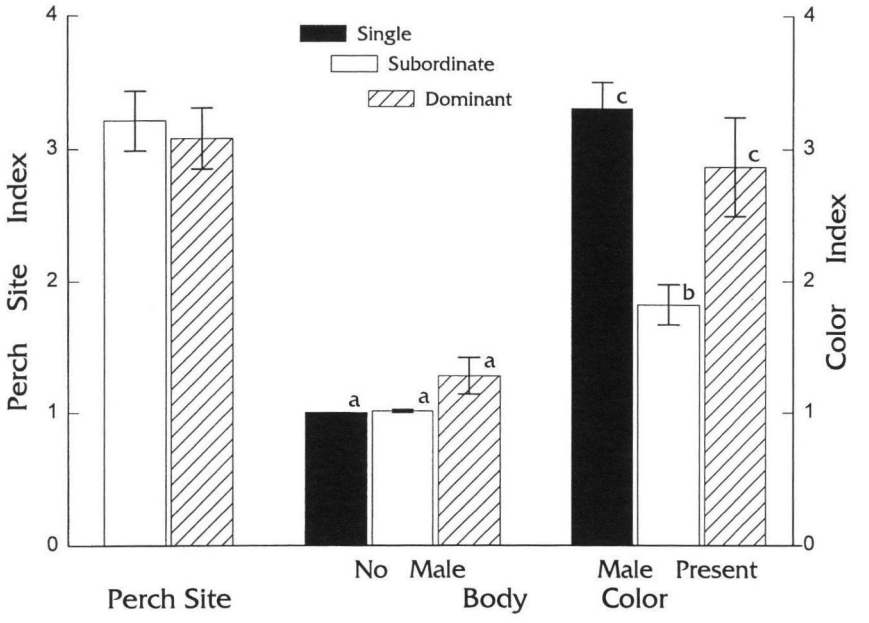

Fig. 4. Mean (± SEM) perch site position and mean (± SEM) body color of dominant and subordinate females. $N = 9$ for both groups. Significant differences are indicated by differing letters (superscript a is significantly different from b and c, and b is different from a and c) just above the mean.

relationships, much as in males (Evans, 1935, 1936a; Greenberg & Noble, 1944; Mason & Adkins, 1976; Greenberg *et al.*, 1984; Greenberg & Crews, 1990). Hypothetically, benefits of dominant status include enhanced acquisition of resources; dominant males have greater access to preferred perch sites (Greenberg & Crews, 1990), mates (Greenberg & Crews, 1990) and food (Greenberg & Noble, 1944; Schoener & Schoener, 1980). The most direct means of additional resource acquisition by dominant individuals is via displacement of other individuals. Displacement occurred frequently among paired females, and were asymmetric among individuals of a pair, but did not result in similar resource partitioning as in males.

Dominant status was established, maintained and reinforced by aggressive displays including assertion, challenge, and fighting, as well as displacement. Isolated females failed to show any aggressive or submissive behavior, suggesting that social behavior is expressed primarily in the presence of conspecific females. Dominant females performed assertion and

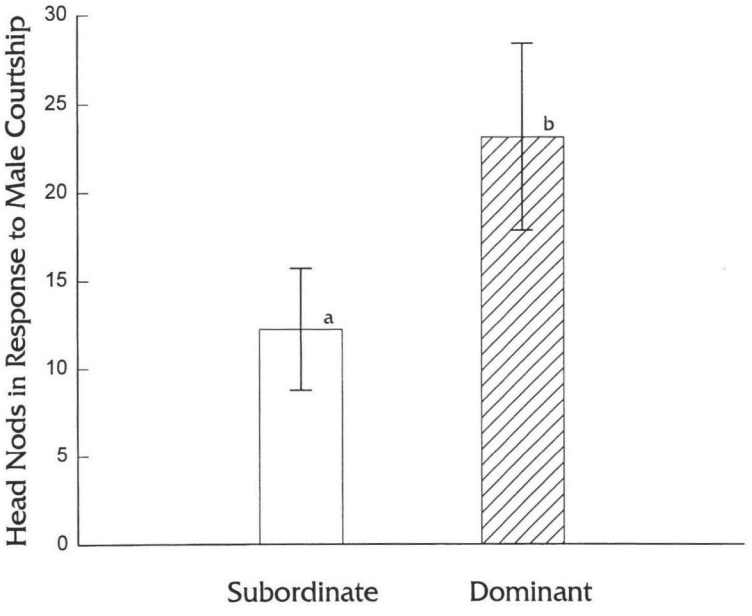

Fig. 5. Mean (± SEM) number of head nods by dominant and subordinate females in response to male courtship displays. $N = 9$ for both groups. Significant differences are indicated by differing letters (a or b) just above the mean.

challenge displays more often than did subordinate females. These displays were followed by attacks and biting of subordinate females by dominant females more often than the reverse. Subordinate females were those which were displaced, and also manifest submissive body posture more often than dominant females. Displacement and lowered posture are characteristic of subordinate females of many taxa, including anoles (Greenberg & Crews, 1990).

Restricted movements or investigation of novel cage areas, access to prey, and time to prey capture were not affected by social status or social interaction. Both paired and control females spent time on the novel cage side, which did not differ significantly between groups or among sampling periods. Although prey availability has been suggested to affect distribution of females in other *Anolis* species (Schoener & Schoener, 1980), prey capturing success was not different between dominant and subordinate females of *A. carolinensis*. Frequent attempts to steal prey were observed;

subordinate females were not inhibited from trying to secure prey, even after it was taken by a dominant female.

Dominant females did not choose different perch sites, although available, from that of subordinate females. Both were usually positioned on the lower half of the perch, which is different from sites selected by male *A. carolinensis* in terraria. Dominant males choose higher perch positions than corresponding subordinate males (Greenberg & Crews, 1990). A possible, although not yet tested, advantage of lower perch site selection by females, dominant and subordinate, may be related to male perch preference and a less obstructed view by potential mates.

Dominant and subordinate females were also not different in mean body color when males were absent. Both groups had a mean body color which was light to moderate green, unlike male *A. carolinensis* in which subordinate males were darker in color (more brown) than dominants (more green) following aggressive interaction (Greenberg *et al.*, 1984; Greenberg & Crews, 1990). The lack of difference in body color by dominant and subordinate females may reflect the lack of male presence, as experiments in which females were housed with males for one month resulted in dominant females with significantly darker color than subordinate females (C.H. Summers *et al.*, 1995). Even subordinate females were significantly darker in the presence of males, as were single females housed with males (Fig. 4). Darker body color, along with lower perch site selection, may indicate submissive social status among females, which may function to regulate social and sexual interactions with males.

Both dominant and subordinate females performed head nods in response to male courtship displays, but the frequency between the two groups was different. Responsive head nodding, indicating receptiveness, was performed significantly more often by dominant females. The results reflect a possible effect of dominant status on access to potential mates. Increased receptiveness to male courtship does not guarantee increased copulations nor increased reproductive fitness, but in light of the relationship between frequency of courtship and copulation rates in males (Greenberg & Lumsden, 1990), these data are suggestive. Dominant males affect the frequency of courting displays by subordinate males. Subordinate males have depressed rates of courtship relative to winners of fights, and subsequently have decreased copulations as well (Greenberg & Crews, 1990).

The significance of the relationship of dominant status to increased responsiveness to male courting is to indicate one function of social status among female *A. carolinensis*; as with males, access to a potential mate is an important part of social and aggressive interaction. Socially and reproductively dominant females, those with established ovarian recrudescence, may be neurochemically more suited to court males and dominate other females. Central serotonergic and dopaminergic systems are simultaneously activated in these dominant females, perhaps reflecting submissive behavior toward males and aggressive interactions with females, respectively (T.R. Summers *et al.*, 1995).

In summary, paired female *Anolis carolinensis* exhibited aggressive social behavior and established dominant-subordinate relationships. One of each pair displaced its cagemate, and manifest increased frequency of assertions, challenges, attacks and biting, with the other more often in submissive posture. Isolated females failed to show any aggressive or submissive behavior. Establishment of social status between paired females appears to have relevance for the acquisition of access to mates. Lower perch site selection and darker skin color in dominant females may be related to increased responsiveness toward male courtship displays. Then, perch, color and responsiveness may facilitate male courtship, and inhibit subordinate females from responding. Female dominant and subordinate relationships are not apparently expressed to the same degree for all resources differently utilized by male pairs. Social status in females may reflect the importance of access to the dominant male.

References

Brackin, M.F. (1978). The relation of rank to physiological state in *Cnemidophorus sexlineatus* dominance hierarchies. — Herpetologica 34, p. 185-191.

Brattstrom, B.H. (1971). Social and thermoregulatory behavior of the bearded dragon, *Amphibolurus barbatus*. — Copeia 1971, p. 484-497.

— — (1974). The evolution of reptilian social behavior. — Amer. Zool. 14, p. 35-51.

Carpenter, C.C. (1960). Aggressive behaviour and social dominance in the six-lined racerunner (*Cnemidophorus sexlineatus*). — Anim. Behav. 8, p. 61-66.

— — (1961). Patterns of social behavior in the desert iguana, *Dipsosaurus dorsalis*. — Copeia 1961, p. 396-405.

— — (1962). Patterns of behavior in two Oklahoma lizards. — Am. Midl. Nat. 67, p. 132-151.

— — (1965). The display of the Cocos Island anole. — Herpetologica 21, p. 256-260.

— — (1967). Aggression and social structure in Iguanid lizards. — In: Lizard ecology: A symposium (W.W. Milstead, ed.). Missouri University Press, Columbia, p. 87-105.

— —, Badham, J.A., & Kimble, B. (1970). Behavior patterns of three species of *Amphibolurus* (Agamidae). — Copeia 1970, p. 497-505.

— — & Grubitz, G. III. (1960). Dominance shifts in the tree lizard (*Urosaurus ornatus* — Iguanidae). — Southwest Nat. 5, p. 123-128.

Crews, D. (1974). Effects of group stability, male-male aggression, and male courtship behavior on environmentally-induced ovarian recrudescence in the lizard, *Anolis carolinensis*. — J. Zool. 172, p. 419-441.

— — (1975). Inter- and intraindividual variation in display patterns in the lizard, *Anolis carolinensis*. — Herpetologica 31, p. 37-47.

— — & Greenberg, N. (1981). Function and causation of social signals in lizards. — Amer. Zool. 21, p. 273-294.

DeCourcy, K.R. & Jenssen, T.A. (1994). Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. — Anim. Behav. 47, p. 251-262.

Evans, L.T. (1935). Winter mating and fighting behavior of *Anolis carolinensis* as induced by pituitary injections. — Copeia 1935, p. 3-6.

— — (1936a). A study of social hierarchy in the lizard *Anolis carolinensis*. — J. Genet. Psychol. 48, p. 88-111.

— — (1936b). Territorial behavior of normal and castrated females of *Anolis carolinensis*. — J. Genet. Psychol. 49, p. 49-60.

— — (1938). Cuban field studies on territoriality of the lizard, *Anolis sagrei*. — J. Comp. Psychol. 25, p. 97-125.

Grassman, M. & Crews, D. (1987). Dominance and reproduction in a parthenogenetic lizard. — Behav. Ecol. Sociobiol. 21, p. 141-147.

Greenberg, B. & Noble, G.K. (1944). Social behavior of the American chameleon (*Anolis carolinensis*). — Physiol. Zool. 17, p. 392-439.

Greenberg, N. (1977). A neuroethological study of display behavior in the lizard *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). — Amer. Zool. 17, p. 191-201.

— —, Chen, T. & Crews, D. (1984). Social status, gonadal state, and the adrenal stress response in the lizard, *Anolis carolinensis*. — Horm. Behav. 18, p. 1-11.

— — & Crews, D. (1990). Endocrine and behavioral responses to aggression and social dominance in the green anole lizard, *Anolis carolinensis*. — Gen. Comp. Endocrinol. 77, p. 246-255.

— — & Lumsden, S. (1990). Social dominance and reproductive activity in the lizard, *Anolis carolinensis*. — Amer. Zool. 30, p. 105A.

Hover, E.L. & Jenssen, T.A. (1976). Descriptive analysis and social correlates of agonistic displays of *Anolis limifrons* (Sauria, Iguanidae). — Behaviour 58, p. 173-191.

Jenssen, T.A. (1970). The ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). — J. Herpetol. 4, p. 1-38.

Licht, P. (1968). Response of the thermal preferendum and heat resistance to thermal acclimation under different photoperiods in the lizard *Anolis carolinensis*. — Am. Midl. Nat. 79, p. 149-158.

— — (1972). Environmental physiology of reptilian breeding cycles: role of temperature. — Gen. Comp. Endocrinol. Suppl. 3, p. 477-488.

Mason, P. & Adkins, E.K. (1976). Hormones and social behavior in the lizard, *Anolis carolinensis*. — Horm. Behav. 7, p. 75-86.

Schoener, T.W. & Schoener, A. (1980). Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. — J. Anim. Ecol. 49, p. 19-53.

Stamps, J.A. (1973). Displays and social organization in female *Anolis aeneus*. — Copeia 1973, p. 264-272.

— — (1976). Rainfall, activity and social behaviour in the lizard *Anolis aeneus*. — Anim. Behav. 24, p. 603-608.

— — & Barlow, G.W. (1973). Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). — Behaviour 47, p. 67-95.

— — & Crews, D. (1976). Seasonal changes in reproduction and social behavior in the lizard *Anolis aeneus*. — Copeia 1976, p. 467-476.

Summers, C.H. & Greenberg, N. (1994). Somatic correlates of adrenergic activity during aggression in the lizard *Anolis carolinensis*. — Horm. Behav. 28, p. 29-40.

— —, Suedkamp, D.A. & Grant, T.L. (1995). Regulation of ovarian recrudescence: Effects of social interaction and size on female lizards, *Anolis carolinensis*. — J. Exp. Zool. 271, p. 235-241.

Summers, T.R., Hunter, A.L. & Summers, C.H. (1995). Social reproductive roles affect central monoamines in female *Anolis carolinensis*. — Soc. Neurosci. Abs. 21, p. 1693.

Tokarz, R.R. (1987). Effects of corticosterone treatment on male aggressive behavior in a lizard (*Anolis sagrei*). — Horm. Behav. 21, p. 358-370.

— — (1995). Importance of androgens in male territorial acquisition in the lizard *Anolis sagrei*: an experimental test. — Anim. Behav. 49, p. 661-669.