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PERCH RESTRICTION AND SEASONAL EFFECTS ON AGGRESSION IN THE IGUANID LIZARD *Anolis carolinensis*

A THESIS

PRESENTED FOR THE

MASTERS OF SCIENCE DEGREE

THE UNIVERSITY OF TENNESSEE, KNOXVILLE

Thomas Alworth

August 1986

ABSTRACT

Available perching space and season interact to influence aggression levels in male _Anolis carolinensis_. Ninety four pairs of adult males were tested over a six-month period (June-November) 1985 in a large enclosure containing either a long or short perch. Aggression levels were recorded for each individual over a three hour period.

Results indicate that both perch availability and season affect aggression levels in males of this species. Animals on the small perch during the months of June, July, and August demonstrated significantly higher levels of aggression than all other lizards. Also, perch sharing was common and often occurred rapidly after an agonistic interaction suggesting this may not be an uncommon event in nature. The data lead me to address the issue of territoriality as it pertains to male _Anolis carolinensis_ and lizards in general. Although most of the lizards in the genus _Anolis_ are described as territorial, I present a theoretical framework in which the "territoriality" of lizards may be regarded as a highly flexible behavioral tactic adaptive only in specific contexts. The broad characterization of a genus or even a species as territorial is misleading.

ACKNOWLEDGMENTS

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1. INTRODUCTION

There is increasing evidence that social organization in many taxa may be dependent on proximate environmental constraints (Brattstrom, 1974) as well as upon evolutionary history. For example, population density (Kaufmann, 1983), perch availability (Brattstrom, 1974), season (Ruby, 1984), and confinement (Evans, 1935; Greenberg and Noble, 1944) have all been identified as factors influencing social organization in lizards.

Most lizards considered territorial in the field (table 1) appear to shift to a hierarchal pattern in the lab (reviewed by Middendorf, 1979). Several species of lizards are also known to shift social structure under varying natural conditions (Evans, 1935; Evans, 1951; Simon, 1975), further indicating the ecological influence on social organization.

The lizard, Anolis carolinensis, is among those described as territorial in the field (Evans, 1935; Greenberg and Noble, 1944; Gordon, 1956; Schoener and Schoener, 1982; Ruby, 1984) and hierarchal in the lab (Evans, 1935; Greenberg and Noble 1944), but remarkably little is known about how such switches in social organization occur, despite extensive and diverse research since the 1930's. This thesis attempts to clarify the effect of perch availability and season

Table 1

Home Range and Territory Size of Various Lizard Species

SPECIES	ADULT SIZE	HOME RANGE (m^2)	TERRITORY (m^2)	AUTHOR
A. acutus	67mm.	1.5	1.5	Philibosian, 1975
A. cristatellus	70mm.	19.0	19.0	Philibosian, 1975
A. aeneus	55mm.	....	8-22	Stamps, 1977
A. sagrei	52mm.	17.6	?	Schoener and Schoener, 1982
A. carolinensis	61.2mm.	32-44	?	Schoener and Schoener, 1982
A. distichus	48mm.	15.6	?	Schoener and Schoener, 1982
A. angusticeps	49mm.	22.0	?	Schoener and Schoener, 1982
A. nebulosus	41mm.	1.5-2.0	1.5-2.0	Jenssen, 1970
A. polylepis	.....	157.0	?	Stamps, 1977
S. jarrovi	55mm.	125.0	?	Simon, 1975
S. jarrovi	54mm.	500.0	?	Ruby, 1978

on spacing patterns and aggression in male _Anolis carolinensis_. Specifically, does limited perch space serve to affect aggression and if so to what extent? To obtain empirical evidence for the importance of space and season on social organization, I introduced pairs of male _Anolis carolinensis_ into a large enclosure and manipulated space by varying perch size. I then measured the distances maintained between paired animals, and recorded aggression levels of each individual. I was concerned with answering specifically the following questions: First, would aggression levels differ due to differences in perch availability? Second, how does season effect both spacing patterns and aggression levels in _Anolis carolinensis_? Third, at what distance from each other would the animals be most aggressive. Also, at what distance would the animals appear to be least aggressive? Fourth, would one animal's presence on the perch affect how another animal utilizes the perch relative to a solitary animal? Finally, I attempted to locate a critical distance for at least the males of this species. By critical distance I mean the minimum distance between two animals necessary to allow both to respect a mutual boundary and thereby reducing aggression within the dyad.

If male _Anolis carolinensis_ are a true territorial animal, that is, the animal defends an exclusive area of an economically defendable size with trespassers being chased when visible (Brown, 1975), I would expect aggression to remain high with little or no perch sharing tolerated in either treatment. If a hierarchy is established, the loser may select a perch at a location where it is tolerated by the winner while exhibiting changes in behavior that are associated with subordinate status indicating that a social hierarchy as been established (Greenberg et al. 1984).

This information allows us to address other important questions. For example, although it has been shown that these animals can "switch" spacing strategies (being territorial in the field while hierarchal in the lab) how quickly do the animals adjust to such changes and by what cues? The second part of this thesis addresses the issue of territoriality as it pertains to Anolis lizards. If A. carolinensis does not defend exclusive territories in the wild, sharing a perch may not be uncommon. If this is true, then what is perceived as "switching" to a hierarchy when confined may in fact not be a switch at all, but, a common strategy seen also in the field but mistaken for territoriality Further, there are several important issues which have become muddled which I will address in this paper concerning space utilization as it pertains to aggression, seasonality, and hierarchal vs. territorial social structures.

2. METHODS

Subjects and Housing

Field fresh *Anolis carolinensis* were obtained from Snake Farm, La Place, Louisiana from June through November 1985. All animals were adult males (snout-vent length (SVL) over 45 mm (Ruby, 1984). Immediately upon arrival the animals were individually and visually isolated in ten gallon vivaria in order to reduce social interactions until the animals were to be tested. The substrate consisted of sphagnum moss and sand, with water provided via water dishes and spraying on a daily basis. Each enclosure contained one wooden perch (42.0 x 2.0 x 1.0 cm) for sleeping and basking, with crickets provided ad libitum. One 40 watt incandescent lamp was suspended over each enclosure to provide a 10L:14D photocycle. Temperature ranged from an evening low of 26 C to a midday high of 32 C stimulating testicular recrudescence in male *Anolis carolinensis* (Licht, 1971). Photoperiod was reduced September through November to 8L:16L to approximate natural light conditions. Animals were marked with a nontoxic marker for individual recognition.

Testing Enclosure

The testing enclosure (143 x 200 x 43cm) consisted of a sliding glass front with the remaining three sides and bottom constructed of wood. The interior was painted with Gliddon

Revere green acrylic latex, and lined with polyethylene plastic to prevent animals from climbing the interior walls. The substrate in the testing enclosure consisted of sand and sphagnum moss while four fluorescent lights provided general illumination. In addition,two 75 watt, 120 volt spotlights were positioned at each end of the enclosure for thermoregulation (fig. 1). Temperature directly beneath the spotlights on the perch was 32 C. while temperature on the substrate was 27 C. The experimental perch was T-shaped and made of wood. The center pole was 60 cm in height, 3 cm in diameter, and was placed at the middle of the enclosure. Its size was held constant between treatments. The top horizontal portion of the perch varied in length, depending on the treatment. In treatment one, the top measured 160 cm in length, whereas in treatment two, it was reduced to 40 cm in length. The entire perch was marked in centimeter increments to facilitate obtaining linear distances between two perching animals regardless of their location. The animals were not fed or watered while in the experimental enclosure, and the perch was washed every 48 hrs to prevent possible chemical communication between subjects.

<u>Procedure</u>

The experiment was divided into two 3-month periods. Summer animals were obtained in June, July and August, while Fall were obtained in September, October, and November.

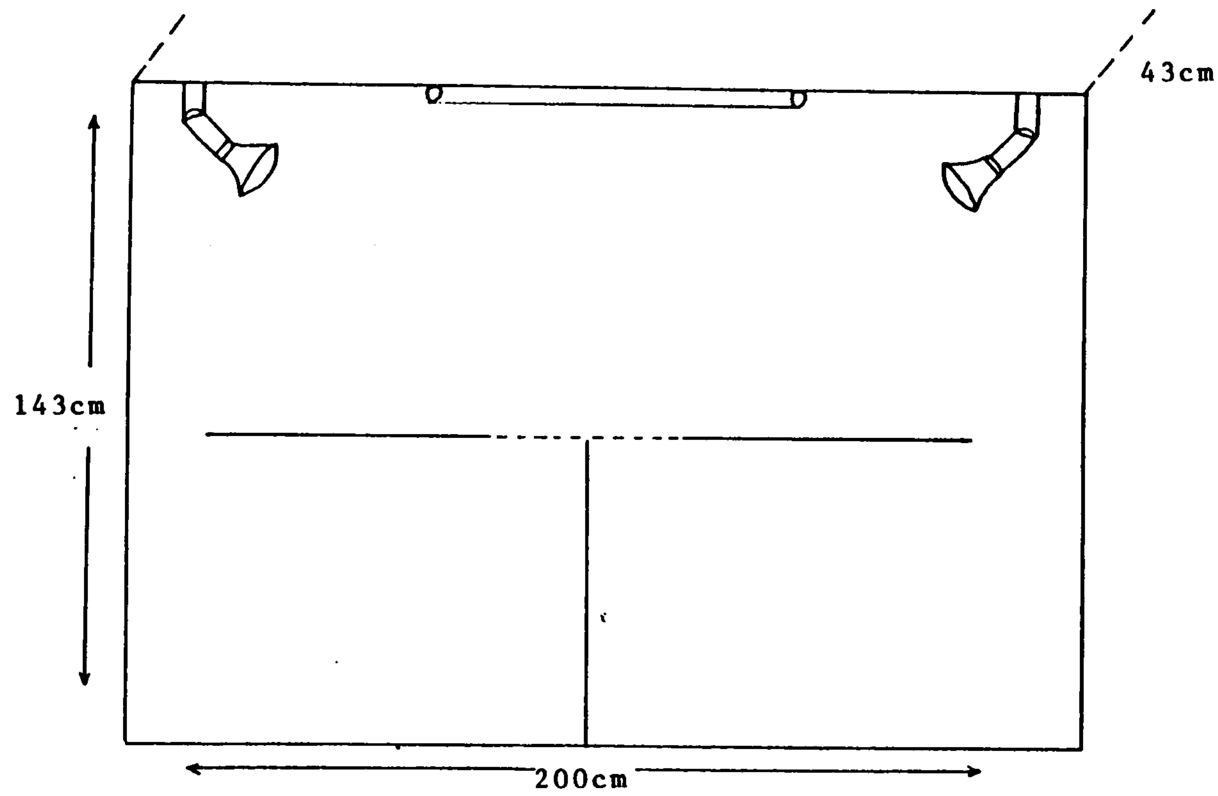


Fig. 1 Testing Enclosure
Short perch, hashed line equals 40cm.
Long perch, hashed line plus top solid line equals 160cm.

Lizards were paired randomly and placed into the experimental enclosure for a 3 hr period in either treatment one (long perch), or treatment two (short perch). Each pair was observed four times at 45 minute intervals with the observer 2 meters from the enclosure behind a burlap blind. Data collected on each pair of lizards included the location of each lizard on the perch as well as the linear distance between them (if either animal was on the substrate, that particular observation was not included in the analysis of the data since accurate measurements of the distance between the animals could only be obtained from the perch). The distance measured was the distance from the tip of the nose of one animal to the tip of the nose of other and was accurate to within one centimeter. Color was scored as green, green/brown or brown since studies by Greenberg et al. (1984) and Greenberg and Crews (1983) seem to indicate that skin color in _Anolis carolinensis_ may reflect social status. Quantifying aggression is extremely difficult since it requires the adoption of arbitrary criteria that may not reflect the animal's real motivation. Male _Anolis carolinensis_ exhibit species-specific behavior patterns in the context of aggressive encounters (Greenberg, 1977) that are stereotypic and sequentially consistant. As a result, the researcher can predict the level of aggression in an individual with some degree of certainty, based on the number of aggressive behaviors (outlined below) exhibited at each observation period.

The following behavior patterns (see also figs. 2 and 3) were each assigned a value of one and, due to sequential dependability, were additive when seen together in an individual.

A) Headnod plus Dewlap

B) Extended Throat

C) Saggital Expansion

D) Eye Spot

E) Jaw Spar

F) Jaw Lock

An animal exhibiting A, B, and C would receive a score of 3. An animal exhibiting A-F would receive a score of 6. If one or both animals were actively displaying when observed, a score of 1 was added to each individual's total for each additional aggressive posture (usually head bobs) until the bout terminated. A bout was considered over when neither animal altered its posture for a period of 30 sec. To assume these behavior patterns and/or morphological characteristics are additive (that is, an animal with a score of 4 is more aggressive than an animal with a score of 2) has been substantiated in the literature (Greenberg and Noble, 1944; Carpenter, 1967; Jenssen, 1977, Losos, 1985).

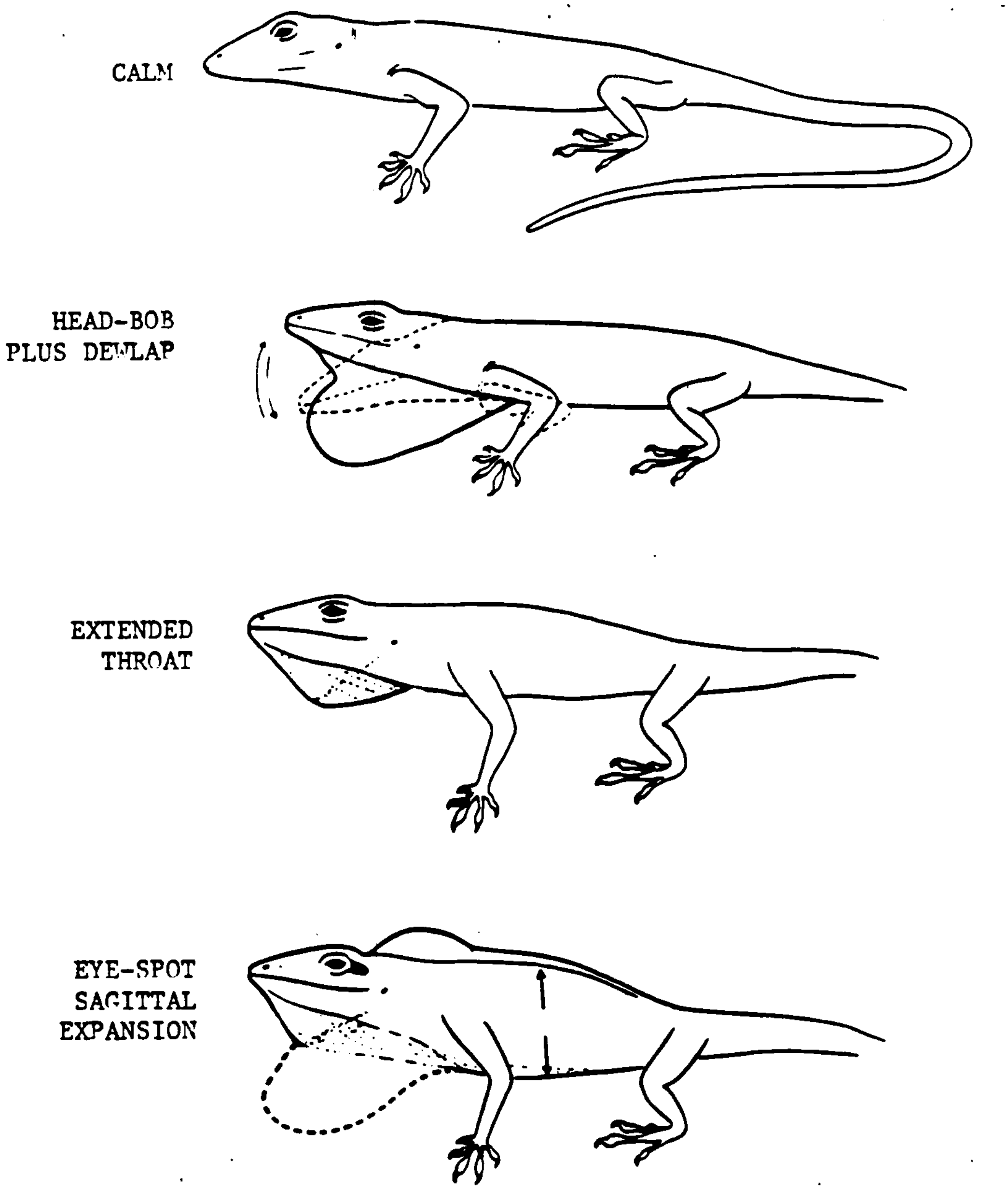


Fig. 2 Postures and morphology denoting aggression in Anolis carolinensis.

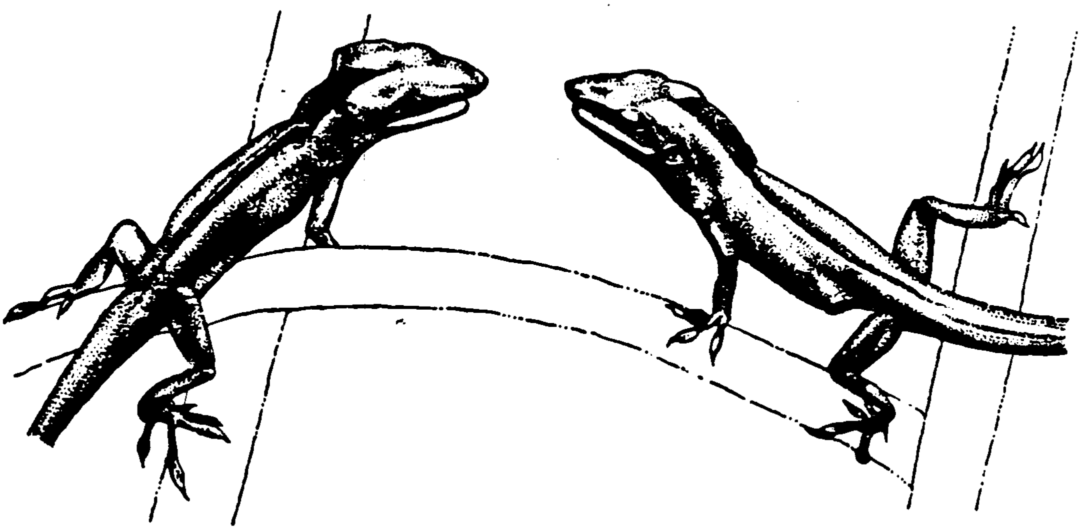


Fig. 3 Jaw-sparring in Anolis carolinensis.

In addition, the following behaviors were observed: 1. supplanting, which I defined as animal A moves towards animal B, animal B retreats (moves away from) A with animal A taking B's original position or occupying a position up to 15 cm beyond B's original position. 2. Chasing, defined as: animal A moves towards animal B with animal B retreating; A follows B at least 15 cm beyond B's original position. Three supplants within 10 seconds were scored as a chase.

3. RESULTS

Lizards on the long perch maintained a mean distance between them of 79 cm during the summer and 83 cm during the fall (see table 2 for C.I.). The small perch prevented dispersal resulting in summer and fall distances of 25 cm and 31 cm, respectively. Although not statistically significant, animals tended to be further away from each other in the fall regardless of perch length (table 2). Levels of aggression on the short perch were significantly higher ($P < .05$; two sample t-test) than on the long perch, but only during the summer (fig. 4). Aggression levels in the fall were also higher on the short perch although not significantly (fig. 5). Aggression was not significantly different seasonally on the long perch (fig. 6). There was, however, significantly less aggression between seasons on the short perch ($P < .05$; two sample t-test) (fig. 7). Seasonal reduction in aggression has been shown in the past in _A. carolinensis_ (Evans 1935; Greenberg and Noble, 1944) as well as a parallel seasonal reduction in testosterone (Licht, 1971), suggesting males are fighting for access to females and not for food. The overall distance between animals when aggressive was highest when animals were less than 5 cm apart but dropped off drastically at approximately 40 cm (fig. 8). Chasing was extremely rare, with only 6 chases recorded out of 299 obsevations on 94 pairs of lizards.

Table 2

Treatment and Seasonal Affects on Distance Between Paired Animals and Aggression.

Treatment (Season)	# Pairs (# Observations)	Mean Distance Between Animals in cm	Mean Aggression
Long Perch (Summer)	22 (66)	78.6 ± 16.9	1.3 ± 0.8
Short Perch (Summer)	25 (75)	25.4 ± 4.5	6.84 ± 3.0
Long Perch (Fall)	22 (70)	82.9 ± 20.2	0.9 ± 1.1
Short Perch (Fall)	25 (88)	31.0 ± 5.7	3.30 ± 2.6

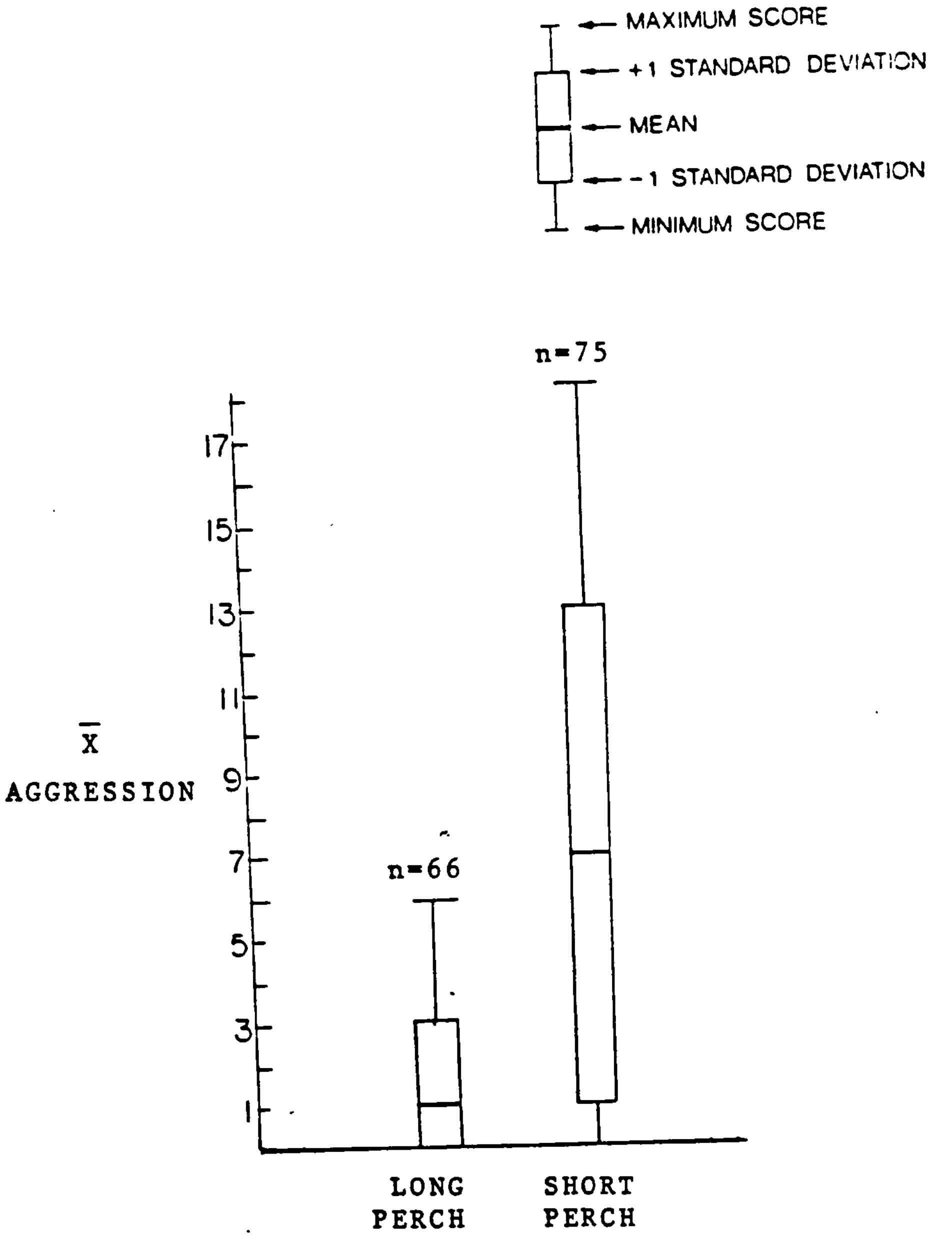


Fig. 4 Mean aggression levels during the summer.
n = number of observations

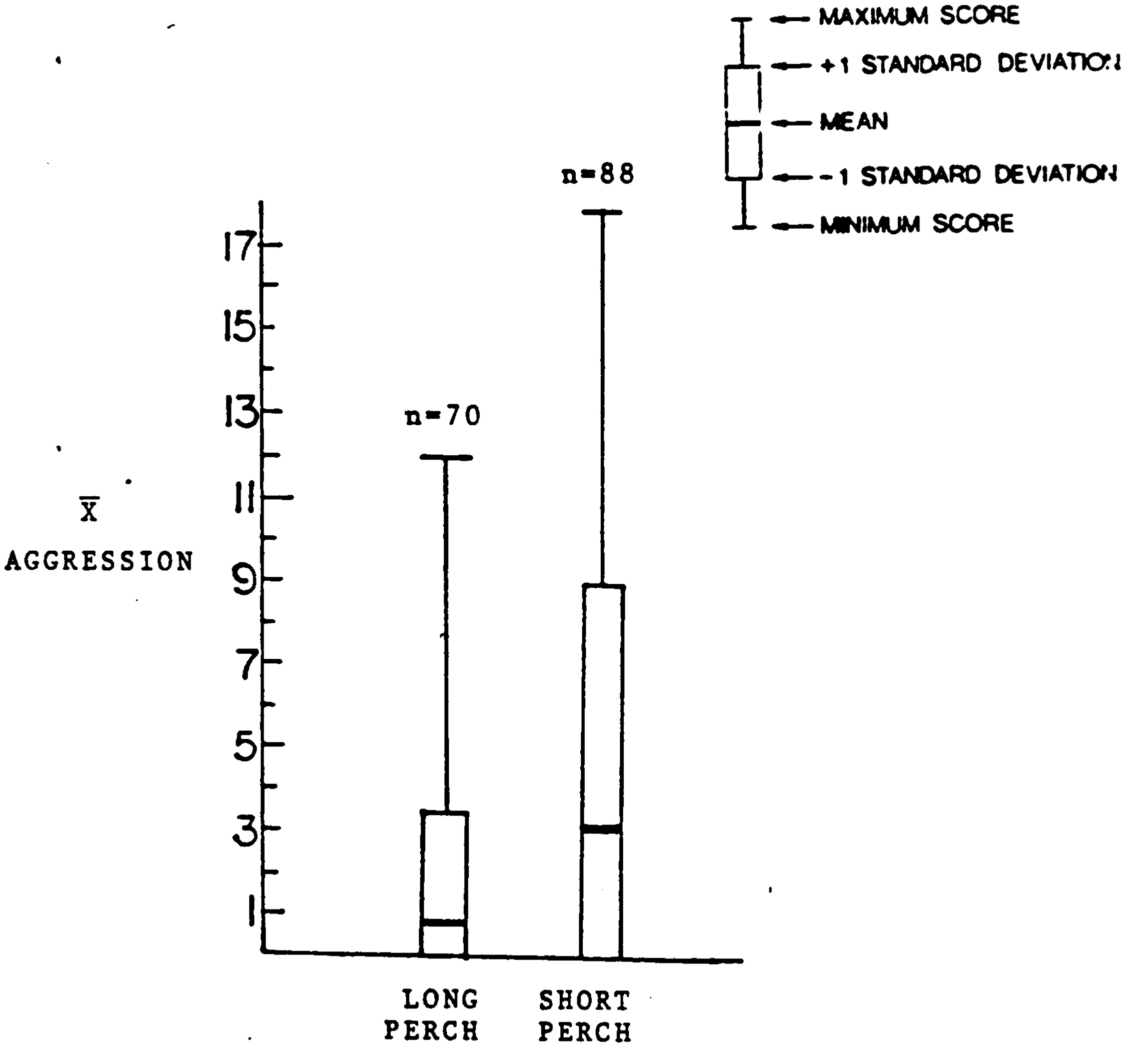


Fig. 5 Mean aggression levels during the fall.
n = number of observations

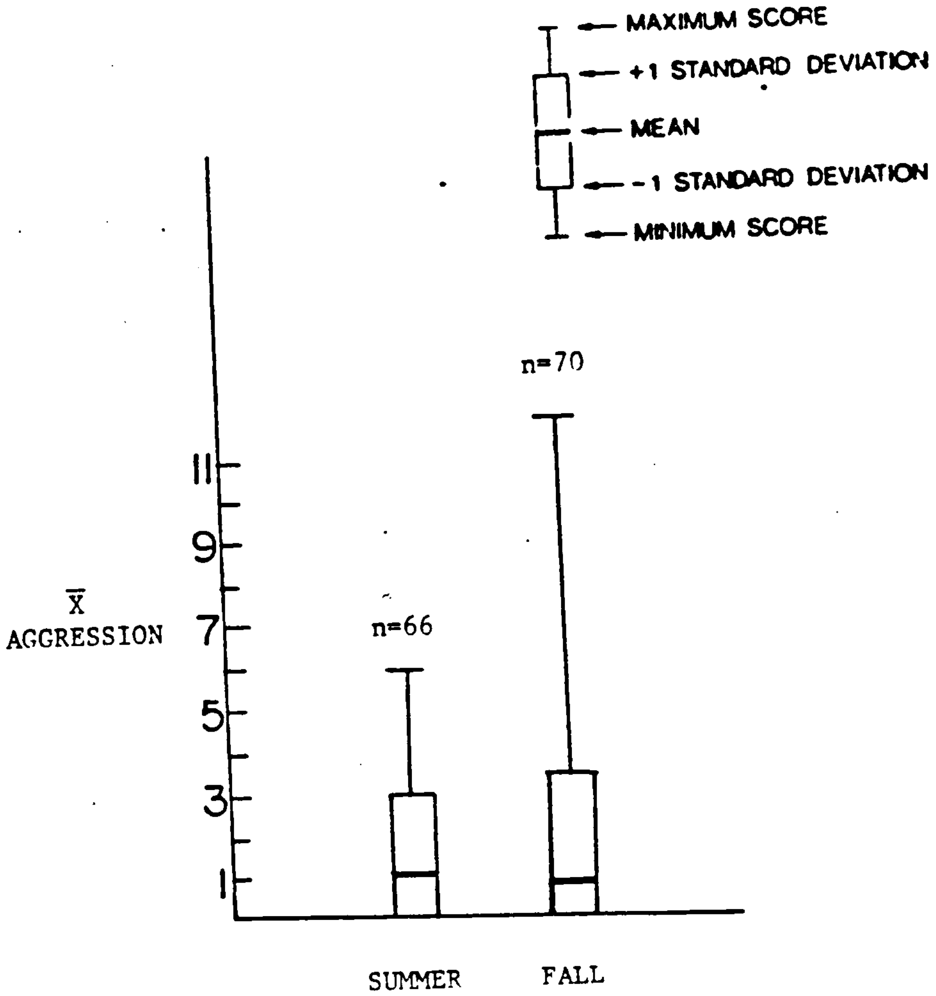


Fig. 6 Mean aggression levels on long perch.
n = number of observations

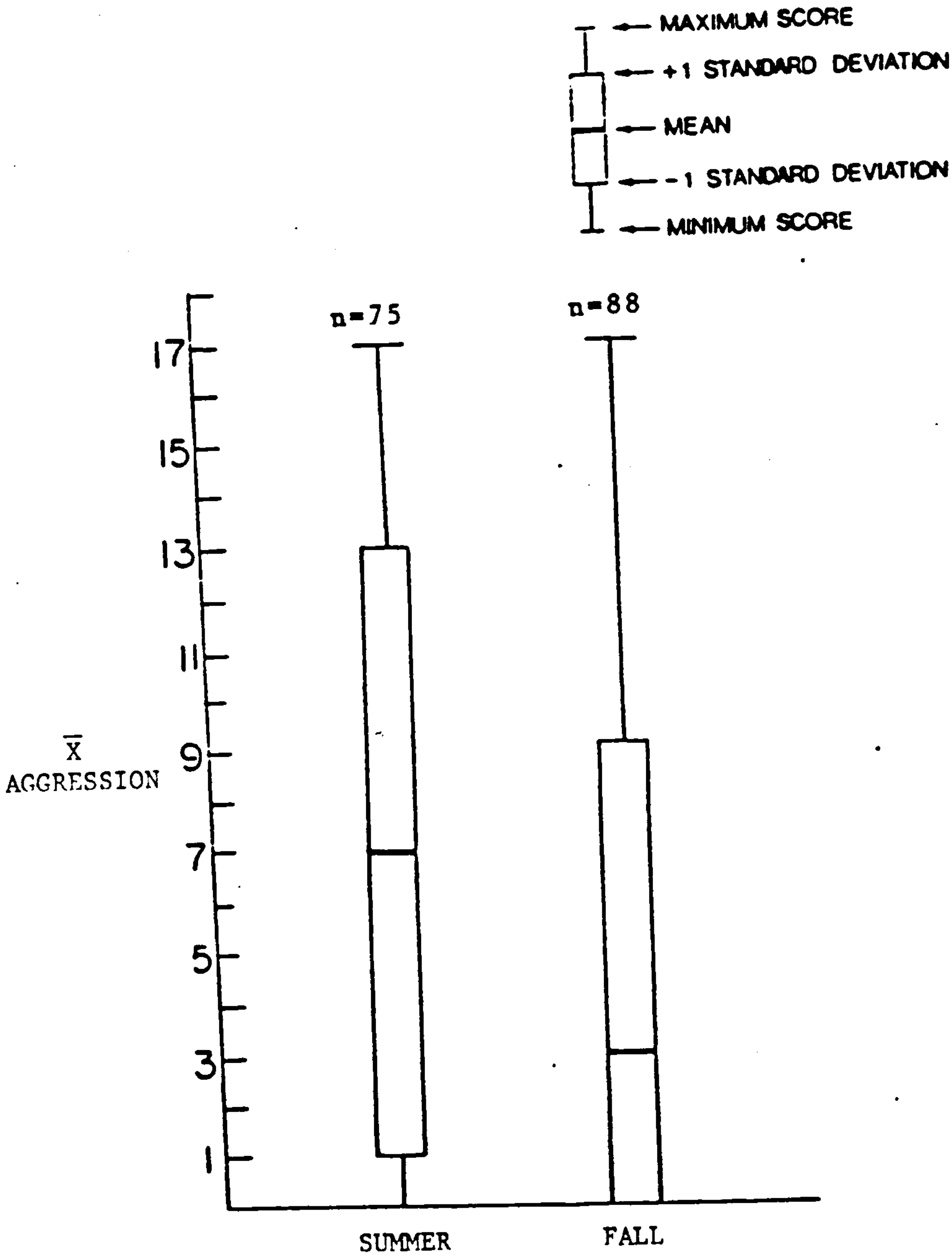


Fig. 7 Mean aggression levels on short perch.
n = number of observations

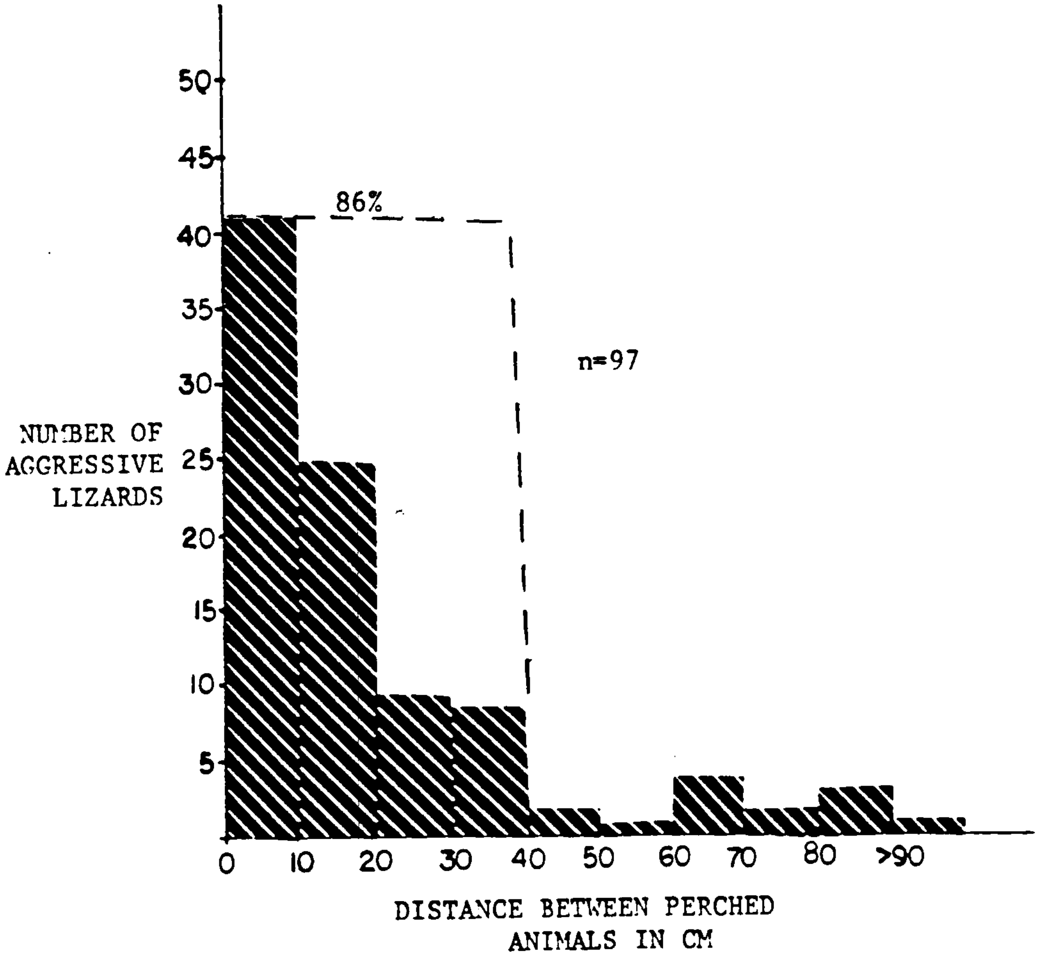


Fig. 8 Distance between perched animals exhibiting aggression for both seasons.

I also was interested in the distances between animals when, firstly, either one or both animals were exhibiting aggression in any form, and secondly, when there was no apparent aggression exhibited by either animal (table 3). On the long perch, the per cent of observations where either or both animals within each pair were aggressive remained consistantly lower than observations where both were passive, independent of the distance between perched animals (fig. 9). However, data from the short perch indicates that when animals were 0-20 cm apart, the per cent of observations with aggression were higher (fig. 10). When the distance between aggressive animals was plotted against the number of observations at each interval, there is an apparent inverse relationship between distance between perched animals and aggression (fig. 11). There also exists an area on the short perch where a the animals were passive most often (30-40 cm) although the animals had 80 cm of perch to utilize (fig. 11). Observations of solitary males revealed that they occupied the top 90% of the time. That is, there is a marked preference for the top over the center pole independent of perch length. Only lizards in treatment two during the summer differed significantly (chi-square = $5.99 < p < 6.66$). Apparently only under these conditions did the presence of one animal inhibit the others use of the top. Neither weight, SVL, or color was a good predictor of which animal utilized the top most. Considering all cases where one animal was on top and the other was on the center pole,

Table 3

Distance Between Perched Animals Both With and Without Aggression.

Treatment (Season)	# Pairs (# Observations)	Mean Dist. Between Animals With Aggression in cm	Mean Dist. Between Animals Without Aggression in cm
Long Perch (Summer)	22 (66)	42.0 ± 20.0	97.0 ± 12.5
Short Perch (Summer)	25 (75)	14.2 ± 4.3	34.0 ± 4.0
Long Perch (Fall)	22 (70)	52.7 ± 26.2	84.6 ± 12.8
Short Perch (Fall)	25 (88)	12.0 ± 8.5	35.2 ± 3.6

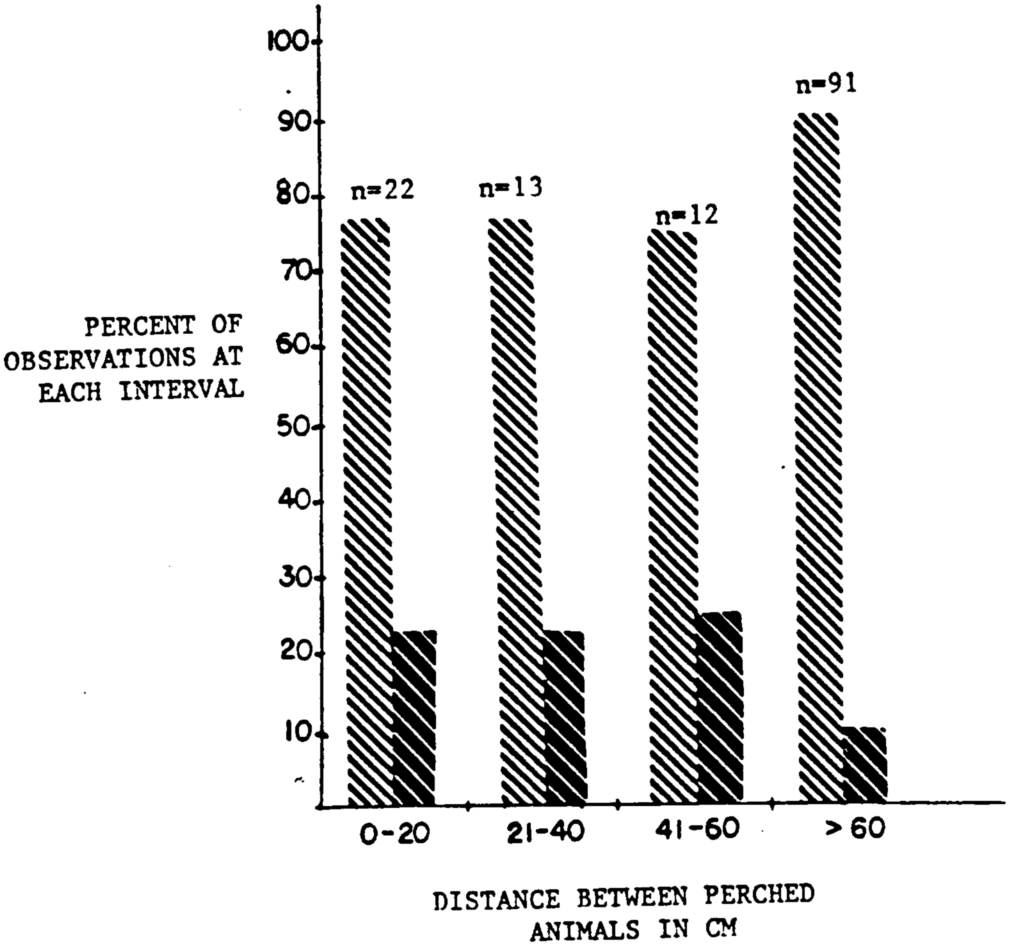


Fig. 9 Distance between perched animals on the long perch for both seasons.

NEITHER ANIMAL AGGRESSIVE

EITHER ANIMAL AGGRESSIVE

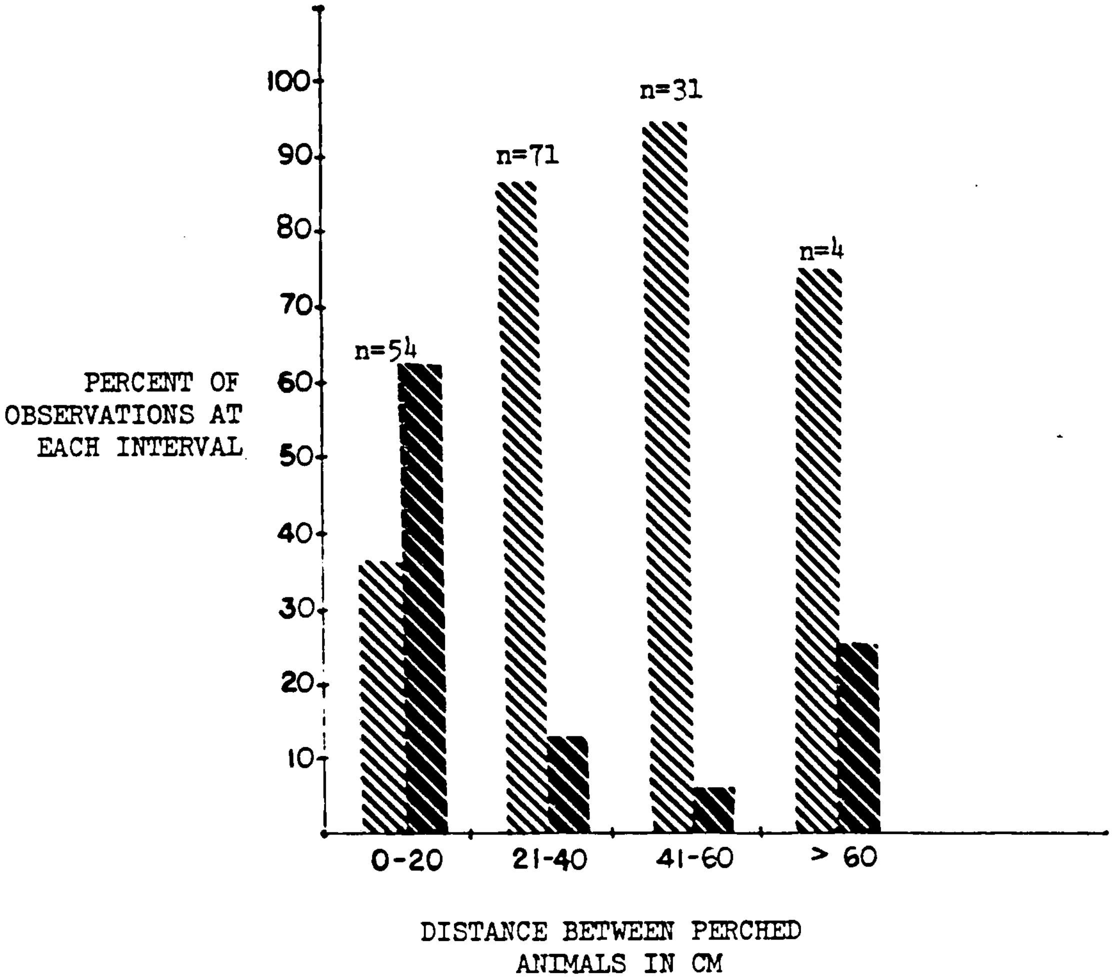
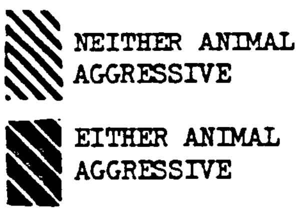


Fig. 10 Distance between perched animals on the short perch for both seasons.



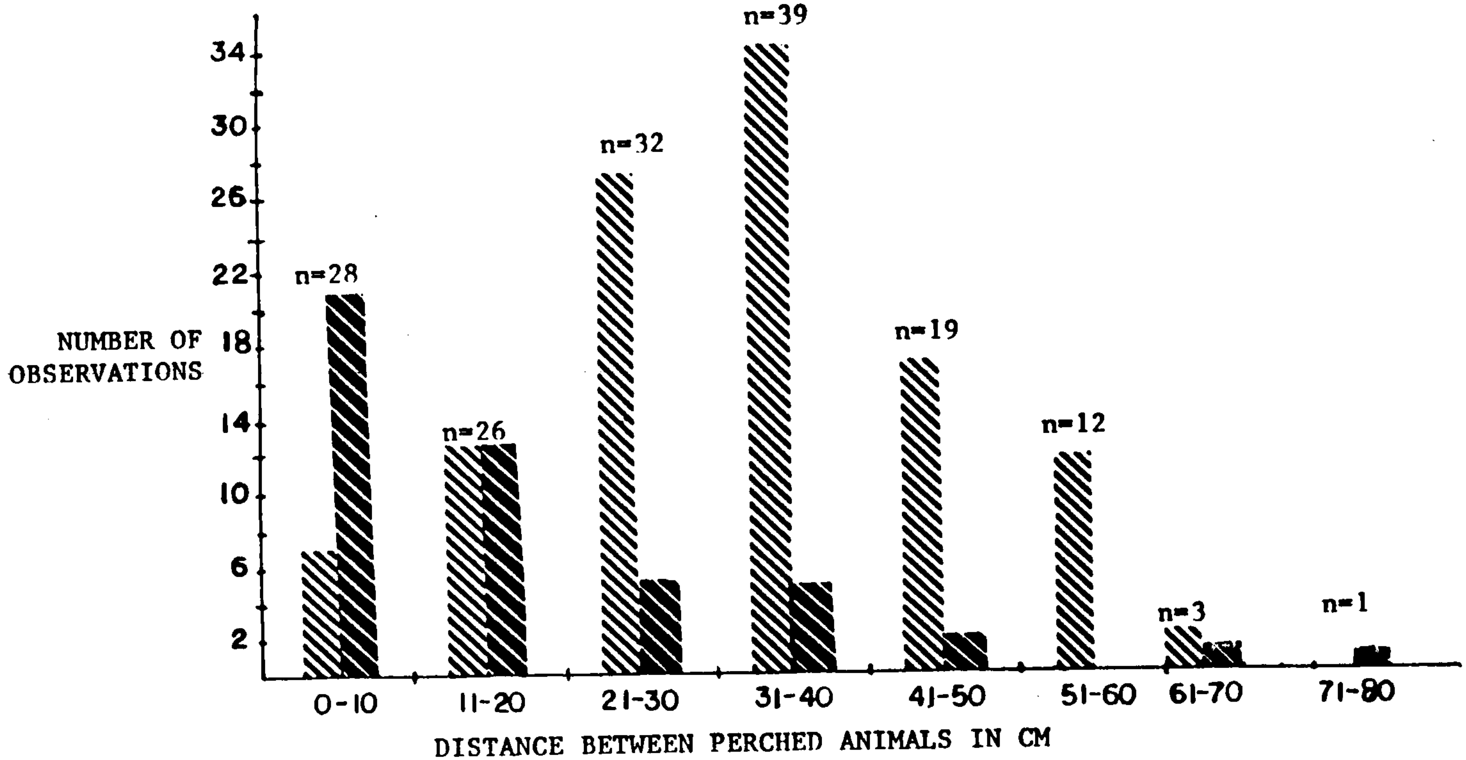


Fig. 11 Distance between perched animals on the short perch for both seasons.

NEITHER ANIMAL AGGRESSIVE

EITHER ANIMAL AGGRESSIVE

47% of the time the lighter animal was on top, while 53% of the time the heavier animal was. The incidence of green or brown animals occupying a higher perching position was nearly identical. When there was both a green and brown animal in the enclosure, the green was perched higher 54% while the brown animal was perched higher 51%.

An analysis of varience indicates that both perch size and season effect levels of aggression in Anolis carolinensis. To accurately predict aggression levels however, one must consider both perch availability and season since there is interaction between the two variables (table 4).

Table 4

ANOVA : The effect of perch size and season on aggression levels in *Anolis carolinensis*.

Response Variable: Aggression

Source of Variation	Sum of Squares	D.F.	Mean Square	F-ratio	Prob(>F)
Main Effects	317.3347	2	158.6673	7.678353	.0008
Perch Size	223.3347	1	223.3347	10.80778	.0014
Season	94.0000	1	94.0000	4.548920	.0357
Perch Size * Season (interaction)	143.7345	1	143.7345	6.955713	.0098
Residual	1859.781	90	20.66424		

4. DISCUSSION

The results of this experiment indicate that restriction of available perching sites will increase aggression levels in male *Anolis carolinensis*. Further, it reinforces the concept of a seasonal effect on aggression and demonstrates the ability of *Anolis carolinensis* to establish hierarchal relationships quickly under laboratory conditions.

Aggression levels were significantly higher on the short perch during the summer months than on the long perch. Lizards on the long perch had a greater opportunity to disperse by utilizing the extreme ends of the perch, but rarely used the substrate or lower site on the perch. Although two individuals were on the top horizontal portion of the perch together, both could often be seen basking passively, usually with approximately 160 cm separating them. Conversely, lizards on the short perch were significantly more aggressive, with one animal usually on top and the other positioned on the center pole (figs. 12-13).

There was no correlation between weight and an animal's perching height, possibly due to the short time period I allowed the animals to interact. This seems contrary to the belief that heavier animals are dominant (Greenberg and Noble, 1944; Boag, 1973; Ruby, 1984; Stamps and Tollestrup, 1984), and that dominant animals perch higher (Evans,1935; Greenberg, et al. 1984). This might be attributable to an artifact of laboratory

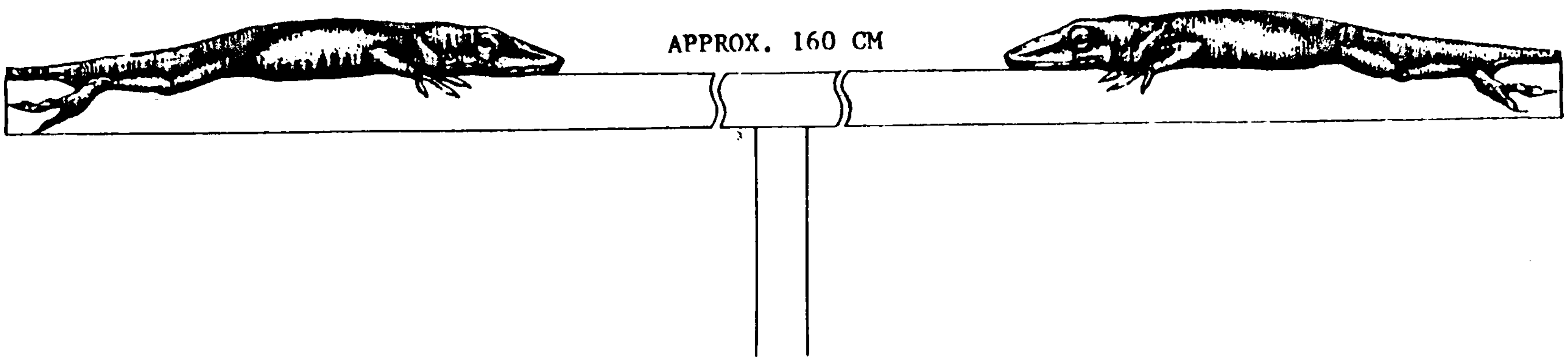


Fig. 12 Perching position and posture common to lizards on large perch.

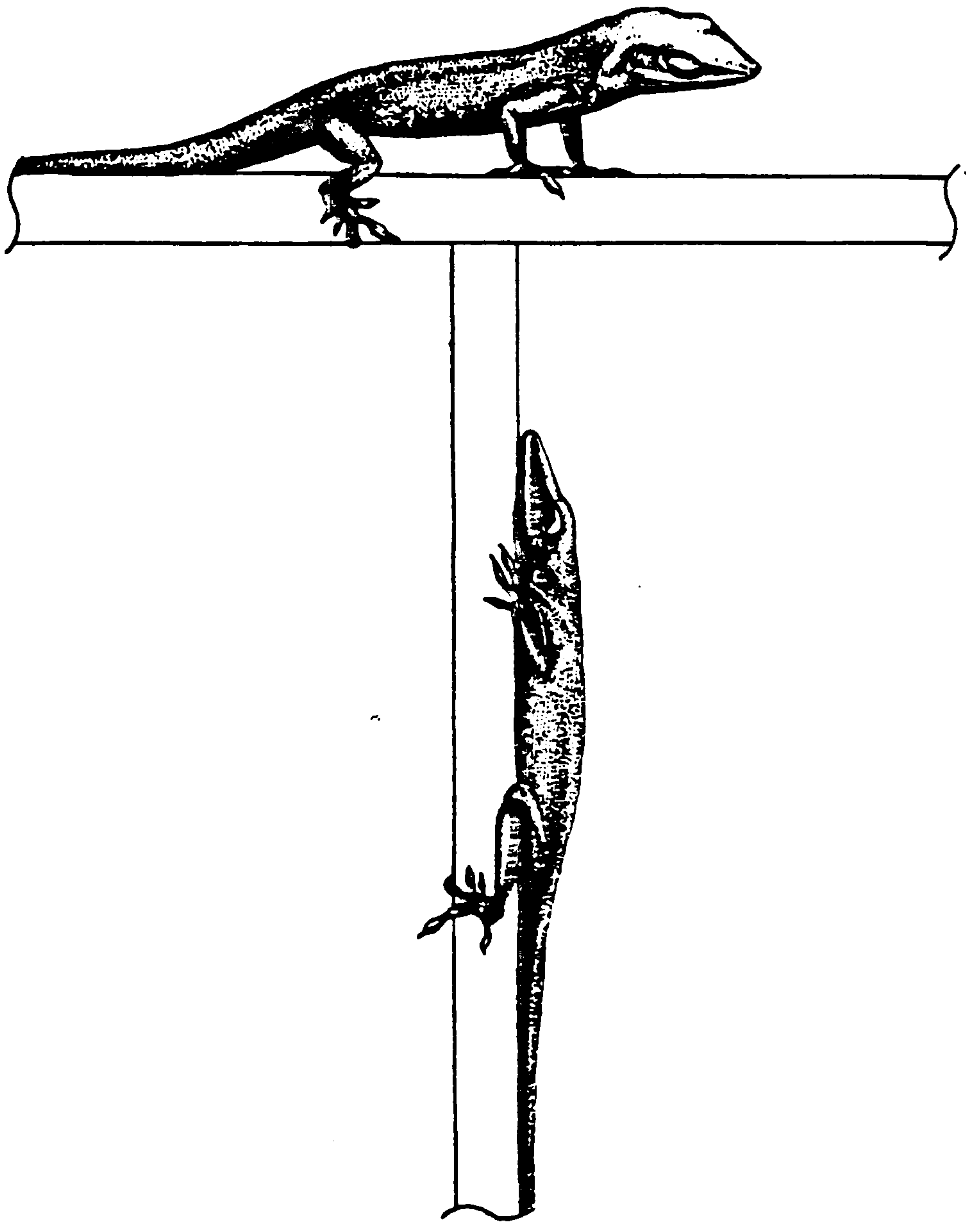


Fig. 13 Perching position and posture common to lizards on short perch.

confinement, in small enclosures dominants may perch higher in order to practice optimal thermoregulation within an enclosure orfor a better vantage point locating prey. In a large enclosure or in nature, relative height may be less important. For example, for an animal at the highest point, foliage may be a visual obstruction conferring a disadvantage in food collecting and/or mate access, while an individual at or near ground level may in fact be better positioned. Also, animals higher in the canopy may be more susceptible to avian predation.

Most high aggression scores were observed when the animals were less than 5 cm apart on the short perch. While still on the perch the animals would orient themselves sideways and display with long bouts of headbobbing and sometimes jawsparring. It was not possible to determine specifically what caused an animal to stop fighting, but inevitably, one individual would slowly descend the perch, sometimes to the substrate. As I have shown, the winner rarely pursues the other, that is, chasing beyond a few centimeters was rare in either treatment. This indicates that complete exclusion from an area is not necessary; tolerance to within a certain distance (approximately 40 cm in my enclosure) is tolerated. Once a winner and loser have been determined as a result of an agonistic encounter, male _Anolis carolinensis_ may be able to remain in close proximity to each other.

Aggression patterns in the fall were similar to summer patterns, however, only half as much aggression was seen in either treatment. Seasonal effects on aggression are not suprising and have been shown by other researchers (Evans, 1935; Fox, 1958; Licht, 1971; Ruby, 1978).

Approximately 84% of all aggression occurred when the animals were, on average, a distance of 40 cm or less apart. When animals were further than 40 cm apart, aggression dropped drastically (fig. 8). Ordinarily, a critical distance is hard to measure due to intraspecific variability in aggression, and in most enclosures would have little external validity. I feel, however, that accurate quantification of the effect of perch space on aggression is clearly revealed by utilizing an experimental design of two perch sizes. By changing only the amount of perch available to the lizards, I could limit space without changing the overall volume of the enclosure. As a result, all lizards had a similar perspective of space (enclosure size) while some only had less perch on which to exploit that area. It should be noted that there were was no vegetation in this enclosure and animals may remain in closer proximity in a more complex environment. It has been suggested that social status may be reflected by color in Anolis carolinensis with dominant animals usually being green while subordinate animals, in very restricted cages, are brown (Greenberg, 1977). Green animals often perch higher and brown animals tend to perch low or remain on the substrate (Greenberg et al., 1984). My results indicate that color and perching height (possibly status) are not correlated. Two possible reasons for this are, firstly, Greenberg conducted most of his work in small enclosures (5-10 gallon vivaria), affording the losing animal little room for dispersal. Secondly, with only 3 hrs of interaction time in my enclosure, possible long term affects of stress would not operate (see Greenberg and Crews, 1983). Aggression is a very robust behavior and it was not uncommon to observe animals behaving aggressively seconds after being introduced simultaneously into the enclosure. Stamps (1984) also found aggression to be intense and prolonged in juvenile Anolis aeneus when the subjects were introduced simultaneously into the testing area. Such behavior is puzzling since specific resources are not yet significant since neither animal has yet had time to evaluate them. In a sense, both animals are intruders into a novel area. Why should "intruders" fight with such intensity when it has been shown that intruders exhibit reduced aggression levels relative to a resident (Stamps, 1984). Male Anolis carolinensis may fight irrespective of location in an attempt to establish superiority, at least within that particular dyad. Subsequent advantages accrued to the winner may include access to females encountered at that location, as well as prey and predator detection due to occupying preferred perch sites.

With the exception of work done by Gordon (1956) and King (1966), both unpublished dissertations, most behavioral work on

Anolis, including my own, has been restricted to the laboratory (Crews, 1974, 1975; Jenssen, 1977; Greenberg, 1977; Greenberg, 1978; Bissinger and Simon, 1979; Cooper, 1979; Greenberg and Crews, 1981; Bels, 1984; Stamps and Tollestrup 1984). That these and some other lizard species can switch to a hierarchal system (Jenssen, 1970; Stamps, 1973; 1977b) raises the question of how common such a social system may be in nature. This problem raises serious questions concerning the validity of referring to *Anolis carolinensis* as a territorial lizard. My work indicates to me that exclusive areas defended against all adult male conspecifics may not represent a common strategy for this species.

As mentioned previously, this species of lizard appears to be capable of switching to a hierarchal social structure when confined. Judging by the ease with which this switch occurred in this experiment, I am suggesting that this change in social structure may not be a switch as a result of captivity at all but instead be a common strategy employed by male *Anolis carolinensis* in the field as well. In the second part of this paper, I present a theoretical framework for supporting the contention that male *Anolis carolinensis* are not a true territorial species and should not be referred to as such.

5. TERRITORIALITY AS IT PERTAINS TO ANOLINE LIZARDS

In a review of the literature on the social structure of *Anolis* lizards, I found that most members of this genus are territorial (reviewed by Stamps, 1977b). Estimates of territory size of various species would permit an assessment of how well my enclosure represents the space necessary for territorial establishment in the lab by male *Anolis carolinensis*. Few authors, however, had data on territory size, although accounts of home range size were numerous (see table 1). This was not a result of the authors failing to collect data on the part of the home range that was defended but, apparently, home range and territory are assumed equal in most *Anolis*. Based on the size of most home ranges (table 1), however, it is unlikely that these animals can effectively defend one in its entirety from intruding males.

Definitions : Old and New

Due to its prevalence across taxa as well as its usefulness, the concept of territory has had imposed on it definitional constraints by various authors. The term territory originated in ornithological literature, resulting ultimately in definition of the various types of territory found in birds as described by Nice (1941) and Hinde (1956). The many definitions of territory have been reviewed in an excellent paper by Kaufmann (1983) in which he expresses his discontent for the concept of dominions presented by Brown (1975) and defined by Wittenberger (1981) which I will discuss later.

"The chief characteristic of territory" says Lorenz (1938) cited in Nice (1941), "is the fact that any individual will fight with more vigor if the combat is decided in his own territory". In the same vein, Tinbergen (1939), cited in Nice (1941), wrote, "A male on his own territory is undefeatable", thus born is the concept of resident advantage. I conducted a correlate experiment with residents of different sizes relative to intruders; of the 10 pairs observed where the resident was smaller than the intruder, the resident lost 8 times. When the resident was larger, however, it won 9 Of 10 trials. These results suggest that residency advantage is not important for successful space defense in Anolis carolinensis.

Brown (1964) brought to the forefront what he called the economic defendability of a territory. A territory must be of a certain size such that the costs of defending do not outweigh the benefits of defense such as access to food, mates, or both. Further, Brown (1975) suggested that trespass into a territory will occur, but the intruder must be driven out upon recognition. The idea of spatiotemporal territory, that is, of an animal defending a certain distance around itself independent of location within its home range, or during a certain time of day or season, was intoduced by Wilson (1975). This definitional variation is not the result of inaccurate observation of territorial behavior, but the result of observing different phenomonon, that is, territoriality in different contexts. Many ornithological studies of territory were conducted on nest builing monogomous bird species such as the Song Sparrow, *Melospiza melodia* (Nice, 1941). These animals have a high investment in an extremely specific area, i.e. the nest site, which is of an economically defendable size. Due to monogamy and long term investment in the site, such as raising young, males would be expected to defend rigorously and would not often be defeated, with trespassers being chased from the area. Under such circumstances, Wilson's (op.cit.) spatiotemporal system is meaningless, and in fact, one would have no basis to assume such a strategy exists. If however such defensive strategies are studied in a different context, namely, a species in which such high investment in one location does not occur, spatiotemporal territories may in fact be a common strategy. Might this be the case in *Anolis* lizards?

Territoriality as it pertains to *Anolis* has been discussed by several authors e.g., (Evans, 1935; Carpenter,1967; Rand 1967; Stamps, 1977 a,b). Most authors, however, have not redefined territoriality as it pertains to anoline behavior. Some authors apparently feel this is not necessary, believing Noble's (1939) definition of "any defended area" is satisfactory (Simon, 1975). However, to assume that the territoriality explains all aggressive encounters with regards to space defense across taxa, is shortsighted and renders the term biologically meaningless.

Why are the animals fighting?

A key consideration often neglected is what are males fighting over? Is it access to food, space, basking sites, females or a combination of any of the above; or is aggression more-or-less controlled by proximate environmental stimuli such as a signal from another male? It would be reasonable to posit a combination, that is, proximate stimuli affected by some attribute of resource availability.

Anolis carolinensis is a sexually dimorphic polygynous species (Schoener and Schoener, 1982) with males being most aggressive during the breeding season (Noble and Greenberg, 1933; Evans, 1935; Greenberg, 1977) triggered by a parallel increase in testosterone (Licht, 1971). Also, aggression is intrasexual, indicating that males are probably competing primarily for females. That *Anolis* males are probably not fighting for food (Stamps,1977a; Ruby, 1984) is not suprising since, being insectivorous, their food source is often variable and not easily defended. Male *Anolis* do compete for basking sites (Carpenter, 1962; Boag, 1973; Greenberg, 1977), however I believe this to be a secondary reason for the majority of aggression seen. It is not reasonable to conceive that male *A. carolinensis* have equal investment in a particular space as does a monogomous, nest building song bird with extended parental care. The question then is, is *A. carolinensis* a territorial species? Trying to "pigeon-hole" a species into an ecological category is not only difficult but possibly inaccurate since few categories are mutually exclusive. With that caution in mind, apparently male *A. carolinensis* (and possibly other *Anolis*) are a promiscuous species, defined as a mating pattern where males and females do not form long term pair bonds and individuals of at least one sex mate with more than one individual of the opposite sex each reproductive season (Wittenberger, 1981). It is important to note that promiscuous does not mean random mating, females are selective but simply do not associate with a male accept for mating. Further, *Anolis caroliensis* apparently exhibit a type of male dominance polygyny as defined by Emlen and Oring (1977). If the operational sex ratio (the number of sexually mature males relative to the number of receptive females in a population) is skewed towards males, male aggression would be high competing for female acquistion (Emlen and Oring, 1977). Since female *Anolis carolinensis* apparently ovulate at approximately 8 day intervals (Andrews, 1985) one would expect asynchronous receptivity among females, another requisite for a male dominance polygyny mating system. I do not mean to infer that *Anolis* lizards form mating leks (an extreme form of male dominance polygyny). I am suggesting, however, that males fight among themselves sorting out rights to females, ultimately determining which will mate if and when a female is encountered.

Fighting for resources that may be limiting sometime in the future has been shown to occur in house cats (Leyhausen, 1965), mountain sheep (Geist, 1971), sage grouse (Wiley, 1973), as well as in at least one species of lizard (Stamps and Tollestrup, 1984). This does not necessarily mean males are defending a particular location into which they will not allow trespass, which Nice (1941) refers to as true territoriality. In fact, male aggression probably occurs throughout each male's home range which could be mistaken for entire home range defense. Although Kaufmann (1983) disagrees, I believe nonexclusion of intruders in ones territory should be referred to as a dominion, defined as a form of spatial organization in which individuals defend nonexclusive use of their home range (Wittenberger,1981). I would expect home range overlap to be extensive since, as I have shown, exclusion is not necessary. There was evidence in my enclosure of subordinate (losing) males staying near the winner even though alternative sites were available. Rarely did the winner actually chase the losing animal from the perch. Upon establishing its agonistic superiority, it appeared to be tolerant, allowing the loser to remain. This would be more likely if the animals were not fighting over space or food but for access to receptive females. When two A. carolinensis males encounter each other, both are likely to behave aggressively. At the termination of agonistic bouts, winners and losers are usually clearly distinguishable. As I have shown, the losing male may then remain in close proximity to the winner. In a preliminary experiment (unpublished data), even lizards with a clear avenue of retreat into comparable "territories" chose to remain in close proximity to the winning male. If a female is encountered, both males may display in an attempt to court (this is being tested by N. Greenberg), however, the winning male is likely to reestablish its dominance, suppressing courtship in the losing individual. I would expect the winning male to then court the female and, if she is receptive, ultimately mate. I believe such a scenario is not uncommon for Anolis carolinensis, but extensive field data are needed to identify the selection pressures acting on both male and, possibly more importantly, females that ultimately shape the social system of this and other Anolis lizards. Although I have stressed the problems in using the term territory, these problems are largely an artifact of the long history of research on the subject and its utility.

Ornithologists investigating the concept as it pertains to birds have had a head start outlining various categories of territoriality within those taxa (Nice, 1941). In time we may find that there exist different categories of territory in Anolis lizards as well. This will not happen quickly as we must first determine, for example, how often and how far males move within their home range. How common is it to find sexually mature males within relatively close proximity to each other and if it does occur, under what environmental conditions? Also, we must learn more about spacing patterns in females. Are they solitary or are they clumped with a hierarchal social structure? Although female parental care is limited to burying the egg, one may hypothesize that females may choose males that occupy areas where egg burying is facilitated or that egg burying sites are superior. The more we learn about constraints on female fecundity, the more accurately we can assess the selection pressures acting on male's contribution to subsequent generations serving to increase their fitness.

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