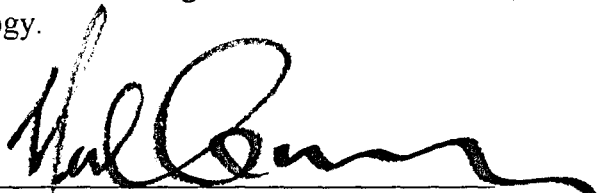


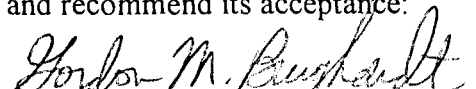
To the Graduate Council:

I am submitting herewith a thesis written by Jennifer Marie Harris entitled "Social Dominance: Effects on Activity and Spacing Patterns on the lizard, *Anolis carolinensis*." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements of the degree of Master of Science, with a major in Ecology and Evolutionary Biology.



Dr. Neil Greenberg, Major Professor

We have read this thesis
and recommend its acceptance:

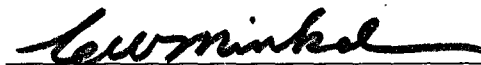


Dr. Gordon M. Burghardt



Dr. Arthur C. Echternacht

Accepted of the Council:



Associate Vice Chancellor and
Dean of the Graduate School

**SOCIAL DOMINANCE:
EFFECTS ON ACTIVITY AND SPACING
PATTERNS ON THE LIZARD,
*ANOLIS CAROLINENSIS***

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Jennifer Marie Harris
May 1999

I am deeply indebted to my advisor, Professor John C. H. Wu, for his guidance and support throughout this project. I also thank my colleagues at the University of Chicago for their helpful comments and suggestions. I am particularly grateful to my friend and colleague, Professor [Name], for his encouragement and advice. I also thank my family for their love and support. Finally, I dedicate this thesis to my mother, [Name], for her unwavering support and belief in me.

DEDICATION

This thesis is dedicated to Julie Sacco, who managed to inspire and motivate me to finish when it seemed like nothing else ever could.

The project I am working on at the University of Chicago is a very challenging one. I have many questions and I need a lot of help. I am grateful to my advisor, Professor [Name], for his guidance and support. I also thank my colleagues at the University of Chicago for their helpful comments and suggestions. I am particularly grateful to my friend and colleague, Professor [Name], for his encouragement and advice. I also thank my family for their love and support. Finally, I dedicate this thesis to my mother, [Name], for her unwavering support and belief in me.

I am also grateful to the University of Chicago for its support and resources. I am particularly grateful to the [Name] Foundation for its support. I also thank the [Name] Foundation for its support. Finally, I dedicate this thesis to my mother, [Name], for her unwavering support and belief in me.

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ABSTRACT

The establishment of a social dominance relationship is known to involve many behavioral changes in its participants. This study was conducted to document the effects of such a relationship on the behavioral patterns of *Anolis carolinensis* males, as well as to examine the nature of the dominance relationship itself. To do this, 13 lizards forming 9 pairs were placed in testing chambers composed of three distinct compartments through which the animals could move freely. In addition to being tested as members of a dominant-subordinate pair, animals were also observed when they were alone in the cages in order to determine a baseline for all the behaviors that were studied. Observations of animals that were in the same compartment with their partner were made separately from those when the animals were in separate compartments and contrasted with each individual's patterns when isolated.

Lizards that did the most patrolling as isolates consistently defeated animals that patrolled less. Males that became dominants showed an increase in patrolling while those that became subordinates showed a decrease. Both dominants and subordinates were found to be less active in the presence of their partners than when they were alone. Subordinates were considerably more active when the dominant males were absent than when they were present. Compared to baseline levels, subordinates showed more submissive postures and lower site selections, but only when they were in the presence of dominants. Subordinates were darker in color when dominants were

present than when they were absent. In both cases they were darker than they had been as isolates. Dominant males tended to enter occupied compartments at higher than expected rates, while subordinates actively avoided entering occupied compartments. Subordinates also avoided spending time in the center compartment of the testing chamber but dominants divided their time relatively equally among the three.

The results of this experiment hinted at several things. First, the fact that dominants show fewer changes from baseline levels than subordinates do suggests that their behavior is closer to "normal" for *A. carolinensis* than is the case with subordinates.

Second, many of the behavioral changes that subordinates display are manifested only when dominants are absent or are different from the changes that occur when dominants are present. Subordinate males are flexible in their responses to social subordination and are capable of responding rapidly to the absences of dominants.

Third, subordinates will actively try to avoid dominants if given the opportunity.

Dominants, however, tend to seek out their partners and make no effort to avoid subordinates. Since the testing chambers were relatively small, subordinates could not escape the presence of the other males and were forced to alter their behaviors in order to coexist with the dominant males. This study indicates that the behavioral changes seen in dominants and subordinates are not due simply to pre-existing individual differences, but rather that they are largely dependent upon the specific roles that the animals have within their social dominance relationship.

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LIST OF ABBREVIATIONS

ACT	Activity Rank Score
PCR	Posture Change Rate
SCR	Site Change Rate
TCC	Total Compartment Changes

CHAPTER I

INTRODUCTION

Social dominance is most commonly defined as a priority of access to some limited resource. Although the term “dominance” can be applied to groups of individuals, entire populations and even to two or more competitive species (Gauthreaux 1978), it is most commonly used to describe a particular association between two members of the same species. Since it is a relationship between two individuals, it is not an absolute property of those animals but rather an *emergent* property that is influenced by numerous traits of those individuals. Singly caged animals are not “dominant” or “subordinate” any more than they are “larger” or “older,” since these terms require a reference to some standard (Bernstein 1981; Bramblett 1981).

History of Social Dominance

The concept of social dominance has been around for nearly 200 years. Dominance orders were first recognized with the work of Pierre Huber on bumblebees (Huber 1802 in Gauthreaux 1978). Hoffer later discovered that the dominance relationship among bumblebees was orderly and predictable (Hoffer 1882 in Gauthreaux 1978). Huber and Hoffer’s work on social dominance went essentially unnoticed by the scientific community for decades, and it was not until the work of Thorleif

Schjelderup-Ebbe that the concept began to attract widespread attention.

Experimenting with chickens, *Gallus domesticus* (Phasianidae) (Schjelderup-Ebbe 1922 in Wilson 1975), and with wild and tame ducks, *Anas boschas* (Anatidae) (Schjelderup-Ebbe 1923 in Wilson 1975), Schjelderup-Ebbe showed that the members of the flocks lived in a highly structured dominance hierarchy. Under this rigid system, every individual responded to the other members of its flock in either a dominant or a subordinate manner. During the course of aggressive interactions, the birds established a “peck order” which determined access to things such as roosts and food. Once this peck order was set up, however, pecking was greatly reduced. At this point, the dominant animal had priority of access over subordinates to desired resources.

After the classic work of Schjelderup-Ebbe, there were numerous efforts to corroborate and expand the concepts of social dominance to other species (reviewed in Wilson 1975; reviewed in Gauthreaux 1978). Schjelderup-Ebbe continued his studies as well, eventually stating that social dominance was one of the fundamental principles of biology (Gauthreaux 1978). During the 1930's, Carl Murchison and his associates made the first attempts to statistically analyze the characteristics that determine rank in individuals. W.C. Allee and his colleagues at the University of Chicago began to study the relationship between hormones and social rank. They came to the conclusion that androgens and rank positions were highly correlated and that high ranking males tended to “psychologically castrate” lower status males (Wilson 1975; Gauthreaux 1978).

Concepts in Social Dominance

In more recent times, there have been numerous attempts to clearly define the concepts of dominance and determine the utility of dominance hierarchies. These questions are made even more difficult by the absence of a common agreement as to how dominance should even be measured (Bernstein 1981). Approaching the issue from a completely different angle, Rowell (1974) stated that "...the concept of dominance has been curiously overrated as a generally governing principle in social behavior..." Departing from the more traditional views, Rowell stated that the entire idea of a dominance relationship was misleading, because it was ultimately *subordinates* that determined and often initiated agonistic interactions. Eschewing the term dominance hierarchy, she instead proposed the phrase "subordinance hierarchy" to better reflect what she considered to be the true nature of the relationship.

Rowell (1974) pointed out that, in most cases, subordinates were the ones that were undergoing changes as a result of social dominance. Therefore, they were ultimately the ones driving the relationship. Noting that "You cannot chase someone who doesn't flee..." she continued on to say that it was the subordinate who had the "decisive" role in the relationship because it actively fled from the dominant, while the dominant made no overt acknowledgement of the subordinate's presence. Pointing out that hierarchies often form in response to stressful situations, she largely discounted most dominance relationships as anything more than artifacts of captivity and equated

subordinate behavior with a direct stress symptom, comparable to an adrenal enlargement.

While it is often true that dominants have behavioral and physiological characteristics comparable to animals housed individually (reviewed in Brain 1981), it would be a mistake to completely disregard the contribution of dominant animals to the relationship. Rowell, in arguing against the use of any concept of social dominance, conceptualizes it as a rigid trait of a unitary motivational nature (Wade 1978). Consequently, data cannot help but fail to fit into such a restrictive definition. The fact that dominance relationships are, by their very nature, dynamic, means that we should not expect perfect stability or predictability from them (Bernstein 1981). The fact that they are a relationship formed between two unique individuals means that, if we wish to truly understand the nature of the relationship, we cannot disregard the input from either member.

Territoriality and Social Dominance

Numerous species have been observed to switch between hierarchies and territories in response to environmental cues (reviewed in Brain 1981; Flannelly and Blanchard 1981; reviewed in Kaufmann 1983). Field studies of lizards have shown that at least a few species will spontaneously shift their social organization from territoriality to a social dominance hierarchy in response to environmental changes (*Ctenosaura pectinata* (Iguanidae): Evans 1951; *Dipsosaurus dorsalis* (Iguanidae): Norris 1953;

Anolis agassiz (Polychridae): Rand et al. 1975). In addition, lizards that are territorial in the field are known to form hierarchies in the laboratory (Carpenter 1967; Brattstrom 1971). Mayhew (1963) noted that two *Amphibolurus pictus* (Agamidae) cohabited peacefully in a small holding tank but, when moved to a larger testing area, one of the animals vigorously pursued the other. He hypothesized that the small (crowded) enclosure inhibited the normal expression of territorial behavior in that species.

Hunsaker and Burrage (1969) suggested that shifts from territoriality to hierarchies would occur whenever territorial animals had limited space available to them and retreat from a given "territory" was not physically possible. Brattstrom (1974) reported that for all territorial species of lizards, crowding resulted in increased social interactions, increased levels of aggression and a shift to hierarchical behavior. This flexibility in behavior indicates that, in many cases, the idea of a "natural" social organization for a particular species is too limited (Brain 1981). Dominance and territoriality should not be thought of as mutually exclusive terms. It is possible for both systems to exist concurrently in nature. Animals are capable of considerable plasticity in their social organizations and can be expected to shift between territorial behavior and social hierarchies in response to environmental stimuli.

Social Dominance and *Anolis carolinensis*

In the laboratory, when paired together, male green anoles, *Anolis carolinensis*, form stable dominant-subordinate relationships. Although such social relationships have not been seen in the field, the speed with which *A. carolinensis* males form this relationship, as well as its apparent stability, suggests a well-established behavioral pattern (Greenberg et al. 1984). Winners of aggressive encounters between two males inhabiting a single enclosure manifest a priority of access to various limited resources, including available females and perch sites. Losers, on the other hand, show little to no interest in females and are readily displaced from perch sites in response to aggressive displays by dominant males.

During the past several years, our laboratory has conducted a considerable amount of research on the green anole. These studies generally involved the use of small glass vivaria, which allowed the researchers to focus on the dominant-subordinate relationship. Studying *A. carolinensis* in these cages has provided several insights into their behaviors as well as the nature of the dominant-subordinate relationship. However, this research, while designed to answer questions on the mechanisms of the stress response, has raised others. For example, it is unclear how much of the behavior of lizards in a dominant-subordinate pair is an attribute of the individuals and how much is secondary to the relationship. Does the social dominance relationship bring about actual changes in behavior or does it simply magnify the differences that already exist?

Although the small vivaria are well-suited to answering certain questions, they are ill-adapted to answer questions raised subsequently. One of the primary problems with these cages is that they restrict the ability of a lizard to avoid a conspecific.

Consequently, the lizards are rarely out of the line of sight of the other animals.

Although this allows researchers to study the lizards under situations of social stress and readily observe them, the cages limit the behavioral options of the animals. It also means that it is not possible to study how a dominant or subordinate behaves when it is not in the presence of its partner. A second problem is the difficulty of knowing which animal is “driving” the relationship. Do dominant males actively search for subordinates and then engage in displays and fights to hold their position, or do subordinates attempt to remain close to dominants and alter their behavior and physiology as a result? Unfortunately, small cages do not provide the ability to answer either of these questions.

Pilot Research

In order to explore these issues, a study was undertaken to examine the behavior of the animals in cages that gave them additional behavioral options. Instead of using the 25 x 25 x 30 cm (L x W x H) vivaria that had typically been used in our lab, a larger, slightly more complex setup was employed. The experimental chamber used for testing consisted of three vivaria (52 x 26 x 30 cm, L x W x H) attached end to end for a total length of 156 cm (Fig. 1). Each of the vivaria was separated by a thin, opaque

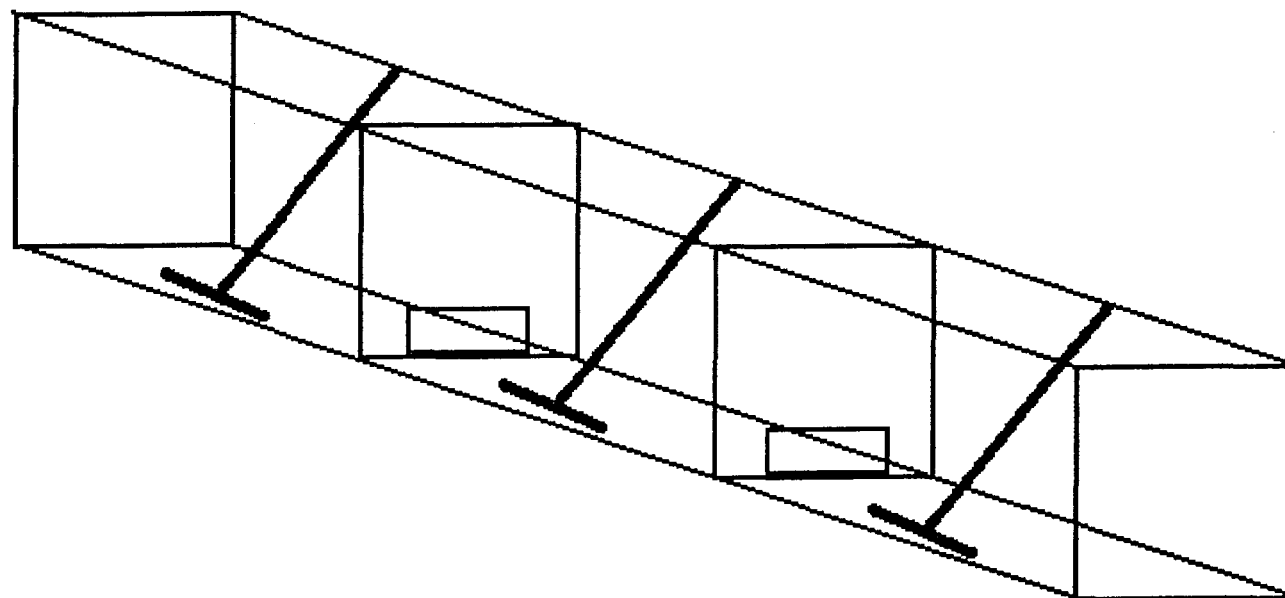


Figure 1: Schematic diagram of the testing chamber used in the experiments.

divider with a small door cut in the bottom to allow access between compartments.

Eight pairs of animals were placed into the large tanks and then allowed to establish stable dominant/subordinate relationships. To gain a clear picture of which animal was driving the relationship, each pair was then watched continuously for seven, 2 hr time periods over a period of 10 to 30 days. During this time, a record was kept of where the animals were located, when they moved between compartments and the number of displays and fights that occurred.

The results of this study hinted at several different things, some of which conflicted with what had been seen in the smaller cages. First, animals that did the most patrolling (moved most frequently between compartments) when they were alone in the testing chamber tended to defeat animals that moved less frequently (Table 1). Second, although dominant lizards in the past had shown few behavioral changes from isolate levels, the dominant males in this study seemed to be showing elevated levels of patrolling as compared to their isolate levels (Table 2). Subordinates, on the other hand, were considerably less active. It was common for them to remain in the same compartment for an entire 2 hr observation. Third, in contrast to the decreased patrolling, the subordinates looked to be slightly more active than usual when the dominants were in separate compartments and generally selected higher perch sites as well (pers. obs.). Fourth, although dominants tended to enter occupied and empty compartments at the expected rates, subordinates showed a strong bias against

Table 1. Number of compartment changes made by each member of a dominant/subordinate pair of *Anolis carolinensis* males when the animals were alone (unpaired) in the testing chambers. The terms pre-dominant and pre-subordinate refer to isolate animals that eventually became dominants or subordinates respectively.

Pair	Compartment Changes	
	Pre-Dominant	Pre-Subordinate
N11----N6	20	63
N6----D8	63	33
P2----P08	44	38
M17----M18	34	26

For each pair of lizards, the dominant member is listed first (i.e. N11 was dominant to N6).

Table 2: Comparison of the number of compartment changes made by individual *Anolis carolinensis* males as isolates, dominants, and subordinates.

Animal	Compartment Changes as A Dominant	Compartment Changes as An Isolate	Compartment Changes as A Subordinate
B08	45	38	1
D8	N/A	33	25
M17	43	34	N/A
M18	N/A	26	6
N6	80	63	49
N11	23	20	N/A
P2	68	44	N/A

Not all animals used in the pilot were observed as isolates.

The term N/A means that a particular animal was not tested in that category (i.e. D8 was never in a testing situation where he was the dominant male).

entering occupied compartments ($X^2=0.79$, 1 df, NS for dominants; $X^2=14.38$, 1 df, $P<0.001$ for subordinates) (Table 3). Finally, the animals appeared to be spending less time together than would be expected based on random chance (Table 4). This last piece of information was the most surprising, since earlier observations had suggested the possibility that animals would spend more time together than expected, not less. However, it was attributed to the fact that, although dominant males divided their time equally among all three compartments, subordinates spent only half as much time in the central compartment as they did either of the end ones (Table 5). This avoidance of the central compartment on the part of the subordinates would mean that they would encounter dominants less often than expected, reducing the amount of time the animals spent together.

Although the pilot study provided a valuable place to begin, it was also flawed in certain ways, which meant the data were potentially biased. First, not all animals were observed at the same time of the day, so natural daily rhythms in activity patterns could have influenced the results. Second, some animals were only studied for a week and a half, while others were paired for a month. Third, only a few animals were studied as isolates in addition to being studied as members of a pair, so it was impossible to do a meaningful analysis of the isolate data. Fourth, the relationship of one of the pairs that was included in the results seemed to change approximately halfway through their trial. Although there was no actual reversal in the roles of

Table 3. Comparison of compartment changes made by *Anolis carolinensis* males into empty or occupied compartments.

Group	Number of Compartment Changes		
	Into Empty	Into Occupied	Total
Dominants	252	114	366
Subordinates	113	25	138

Based on random chance, animals should enter empty compartments twice as often as occupied ones (Empty to Empty + Occupied to Empty vs. Empty to Occupied). Dominants entered empty compartments twice as often as occupied ones. Subordinates entered empty compartments *four* times as often as occupied ones.

Table 4. Amount of time dominant and subordinate *Anolis carolinensis* males spent in the same compartment of the testing chamber.

	Time Spent Together in Same Compartment		
	Total Minutes	Average Min/ Trial *	Percentage
Observed	1803	32.2	26.71
Expected**	2250	40	33.33

* Trials lasted 120 min
** Based on random chance, animals would be expected to spend 1/3 of their time together in the same compartment

Table 5. Percentage of time dominant and subordinate *Anolis carolinensis* males spent in each of the three compartments of the testing chambers.

Group	Percent Time in Each Compartment		
	Left	Center	Right
Dominants	34.18	33.35	32.47
Subordinates	41.14	19.24	39.63

dominant and subordinate, the “dominant” lizard showed no interest in either the “subordinate” male or in introduced females. At that stage, his position as “dominant” for the rest of the trial was based on his previous behavior rather than the way he acted from that point to the end. Finally, the animals were studied between the months of August and February, when animals in the wild would not normally be showing territorial or reproductive behavior. Although the lizards were under a light regime designed to maintain their hormones at breeding season levels, the fact remains that the behaviors being studied would not normally be expected to occur during that time of year.

In order to gain a clearer picture as to what was actually going on with the animals, the experiment was repeated and improved. First, all lizards were tested as isolates in addition to being tested as members of a pair. Second, several additional variables were included in the experiment that had not been looked at during the course of the pilot study. Third, data were gathered at a time intended to coincide with the normal breeding season of the lizards (April-August). Fourth, all animals were observed during the same time of the day and received several observations in addition to the 2 hr blocks. Fifth, any pair of animals where either a reversal in positions or a “crash” (when neither animal was dominant or subordinate) occurred were excluded from the final analysis.

Pre-Existing Differences in the Behaviors of Unpaired (Isolate)

Animals

The first thing that I wanted to determine was whether or not certain animals were more likely to become dominants, while others were more likely to become subordinates. Since dominance is an emergent property and not an intrinsic characteristic of the animal itself, the question being asked was not whether or not certain animals were inherently dominant or subordinate. Previous research in our lab had shown that a lizard could be dominant to one animal and subordinate to another, so I already knew that being a dominant lizard was not an innate attribute of the animal. Instead, the issue was whether or not there were some measurable traits that could be used to predict which animals were likely to defeat others in agonistic encounters.

For many species, an animal's size is thought to be an important factor in determining whether or not it will win an encounter with a conspecific. Generally, bigger animals are expected to defeat smaller animals (reviewed in Robinson 1986). Afterwards, they should either force the loser from the territory or assume a dominant role in the relationship. However, the majority of the lizards in our laboratory are relatively close in size, so this aspect is not as likely to play an important role in determining the outcome of contests between individuals.

Garland et al. (1990), using the lizard *Sceloporus occidentalis* (Phrynosomatidae), discovered a positive correlation between the locomotor speed of the lizards and social dominance. They found that the lizards that won dyadic encounters had significantly higher sprint speeds than did the losers of the encounters. These findings are similar to the results found in the pilot study for this research. In the preliminary research, the rate at which a lizard moved through the testing chamber as an isolate animal seemed to be related to the outcome of agonistic encounters with other males. In three out of four trials where the isolate compartment change rate was known for both participants, the animal with the highest number of compartment changes won the encounter.

The Effects of Social Dominance on the Green Anole

There has been considerable work on the neurobiology and physiology of *A. carolinensis*, particularly with regards to the stress response (Greenberg 1990; Greenberg & Crews 1990; Greenberg et al. 1984). Other experiments have examined the effects of social dominance and stress on the behavior of this species (Greenberg et al. 1984; Greenberg and Chen 1987; Greenberg and Crews 1990). In most of the studies, the behavior of the dominant animal has not appeared to change greatly from what it was before pairing. The subordinate animals, however, have repeatedly shown several obvious shifts in behavior from their isolate levels. These changes include lower perch sites, more submissive postures, reduced aggression, depressed rates of courtship and considerably darker body colors as compared to their normal, isolate

levels (Greenberg 1977; Greenberg et al. 1984; Greenberg and Crews 1990; Greenberg and Lumsden 1990).

The present research differs from previous studies in several ways. First, it attempted to describe the behaviors of the animals when they were separated from their partners as well as when they were in close proximity to them. Second, the study focused heavily on the activity levels of the animals under the various testing conditions, an aspect that had received little attention in previous experiments. Finally, I examined several lizards serving as both dominant males in one relationship and as subordinate males in other relationships. This was done to document that any changes seen in behavior were not simply due to individual differences, but were dependent upon the specific "role" the animal had within the relationship.

In addition to looking at the changes that occur in members of a dominant-subordinate relationship, this study also focused on the nature of the relationship itself. Specifically, I attempted to determine if the animals avoided one another or if they were attracted to each other. In order to accomplish this objective, I examined not only the amount of time that animals spent together, but also the pattern of their movements between empty and occupied compartments.

Hypotheses

PRE-EXISTING DIFFERENCES IN THE BEHAVIORS OF UNPAIRED (ISOLATE) ANIMALS

Are there any significant differences between the activity levels of animals that eventually become dominants and those that become subordinates?

H₀: There are no differences between the activity levels of animals that eventually become dominants and those that become subordinates.

H₀: There are differences between the activity levels of animals that eventually become dominants and those that become subordinates. Animals that are the most active (as isolates) will be able to defeat animals that are less active.

THE EFFECTS OF SOCIAL DOMINANCE ON A GREEN ANOLE

Does the behavior of an animal in a social dominance relationship change from its baseline, isolate levels?

H₀: The behavior of an animal that becomes a dominant does not change from its baseline isolate levels.

H₁: Dominants will show elevated levels of compartment changes as compared to their baseline, isolate levels

H₀: The behavior of an animal that becomes a subordinate does not change from its baseline isolate levels.

H₁: Subordinates will show decreased levels of activity, darker body colors, more submissive postures and lower perch sites as compared to their baseline, isolate levels.

Do animals in a social dominance relationship behave the same no matter where their partners are or do their behaviors change when they are alone?

H₀: Dominant males do not behave any differently when their partners are present in the same compartment than they do when the subordinates are absent.

H₁: Dominant males behave differently when their partners are present in the same compartment than they do when the subordinates are absent.

H₀: Subordinate males do not behave any differently when their partners are present in the same compartment than they do when the dominants are absent.

H₁: Subordinate males will show lower levels of activity, more submissive postures and select lower perch sites when their partners are present in the same compartment than they do when the dominants are absent.

Given a testing situation where the animals are able to move away from each other, will they actively try to seek each other out, avoid each other as much as possible, or simply move through the testing chamber randomly?

H₀: Dominants will move through the testing chamber randomly, neither seeking out nor avoiding subordinates.

H₀: Dominants will not move through the testing chamber randomly but will actively seek out subordinates.

H₀: Subordinates will move through the testing chamber randomly, neither seeking out nor avoiding dominants.

H₀: Subordinates will not move through the testing chamber randomly but will actively avoid dominants.

H₀: Dominants will divide their time equally among the three compartments.

H₁: Dominants will not divide their time equally among the three compartments.

H₀: Subordinates will divide their time equally among the three compartments.

H₁: Subordinates will avoid the center compartment.

CHAPTER II

METHODS

The data for this study were collected from April 1994 through mid August 1994, using adult male *Anolis carolinensis* commercially supplied by the Snake Farm, LaPlace, Louisiana. Lizards were placed in habitats under conditions known to initiate and maintain gonadal recrudescence throughout the year (Crews and Garrick 1970; Crews et al. 1974; Licht 1967; Licht 1971). The stimulatory regimen had a photic cycle of 14 hr light:10 hr dark (0630-2030), which provided daily temperature fluctuations of 22-32°C.

The thirteen males used for this experiment were chosen at random from the pool of available animals (see Table 6 and Table 7 for sizes). Prior to any behavioral experimentation, animals were isolated for a minimum of seven days in glass vivaria (25 x 25 x 30 cm, L x W x H) that contained a 20-cm diagonal perch and a substrate of sphagnum moss. The animals were fed crickets three times a week and given water ad libitum. Handling was minimized to reduce this as a potential stressor (Meier et al. 1973).

Table 6. Sizes of ISOLATE *Anolis carolinensis* males.

Animal	SVL (mm)	Mass (g)
M1	62	4.95
M4	66	5.51
M5	64	5.71
M9	62	5.31
M10	65	5.83
M13	63	5.32
M21	62	5.18
M31	60	4.48
M33	64	5.47
M43	59	4.44
M51	62	5.22
S2	61	4.90
S3	61	5.14
AVERAGE	62.50	5.19

SVL = snout-vent length

Table 7. Sizes of PAIRED *Anolis carolinensis* males.

Pairs	Dominants		Subordinates	
	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)
M5----M4	64	5.64	66	5.62
M1----M9	62	4.92	63	5.34
M10----M31	65	5.82	60	4.39
M13----S3	63	5.37	62	5.27
M51----M1	62	5.18	62	5.00
M33----M43	64	5.68	60	4.58
M4----M10	66	5.67	65	5.75
S3----M21	61	5.08	63	5.36
M9----S2	62	5.24	61	4.90
Average	63.22	5.40	62.44	5.13

SVL = snout-vent length

For each pair of animals, the dominant partner is listed first (e.g., M5 was dominant to M4).

Behavioral Techniques

Each male selected for testing was briefly exposed to a receptive female to determine willingness to court. Tests were stopped after five minutes or if copulation or a fight seemed imminent. Since failure to court a female is one of the defining characteristics of subordinate males, only males that passed this test were used in the experiments. Males that failed to court were tested again at a later date and used if they passed at that time.

The experimental chamber used for testing was the same as had been used in the pilot study for this research (see Fig. 1). The testing chamber was made up of three vivaria (52 x 26 x 30 cm, L x W x H) attached end to end. A thin, opaque divider separated each vivarium. Small doors cut in the bottom of the dividers allowed access between compartments. Each compartment contained a centrally located perch, a small amount of sphagnum moss to cover the floor and a source of fresh water. Except for the fact that the central compartment had two doors instead of one, the compartments were identical.

All animals were tested a minimum of two times: once as an isolate and once as a member of a pair. Lizards were placed into opposite end compartments of the experimental chamber and then left alone for three days before any observations were recorded. This allowed them to adjust to the novel environment and, in the case of the paired animals, to allow dominance relationships to form and stabilize. Since the

animal that wins the initial encounter is not always the ultimate “winner” in the relationship, no serious attempt was made to determine the positions of “dominant” or “subordinate” until after the animals had been together for three days.

Each trial took between 10 to 17 days, with most taking 12 days. Once all observations had been made for a given trial, the animals were removed from the testing chamber and returned to their individual vivaria. Pilot studies had indicated that winning or losing an encounter had no effect on an animal’s ability to win a later encounter with another lizard, as long as sufficient time had passed for hormonal levels to return to normal, baseline levels. The hormone levels of the subordinates were considered to have returned to normal once the animals resumed courtship behaviors, however the dominants return to baseline levels weren’t quite as obvious. The amount of time that was determined to be required for these animals to “recover” was based on the work of Greenberg and Crews (1990). These researchers found that, although winners of agonistic contents had elevated levels of androgen one hour after a fight, the levels had returned to near control levels by one week. Therefore, after at least one week had passed, animals were considered eligible for testing again. The thirteen lizards that were used were combined to form nine pairs, with five animals serving as both dominant to one animal and subordinate to another. The only restriction that was placed on using an animal again was that it not take on the same “role” in the pairing twice (i.e., it could not be a dominant animal twice).

DETERMINATION OF DOMINANCE AND SUBORDINANCE

There are several methods available for determining which animal is the "dominant" and which is the "subordinate" for *A. carolinensis*. Generally, subordinates are noticeably darker than the dominant, they tend to adopt lower perch sites and they adopt submissive, head-down postures (Greenberg and Crews 1990). These variables were used as indicators of subordination, but they were not used as definitive characteristics. In most cases, dominants were easily identified by their displays and by the fact that, after the third day, subordinates repeatedly fled from those displays. In the few instances where it was not possible to determine the dominant animal in this manner, a female was introduced into a compartment containing both males. The male that courted the female was considered to be the dominant animal. There were a few cases where neither lizard showed aggressiveness towards the other or interest in females. Since social dominance is defined as one animal having a priority of access to resources over another animal, it was not possible to consider either male "dominant" in these situations. Therefore, both lizards were removed from the testing chamber and replaced with new animals.

Methods of Observation

Observations began approximately 2½ hours after the lights first came on and ended 1½ hours before they were turned off for the night. Beginning on the fourth day, data were collected in the following manner.

CONTINUOUS OBSERVATIONS

(A) Using a video camera, each lizard was observed for seven, 2 hr periods. The camera was operated by remote and could be zoomed in and out as well as rotated from side to side in order to focus on the animals. Data were taken concerning the location of the anoles within the experimental chamber, noting the length of time spent in each compartment, and the timing of movements between the compartments. These observations took place between 0900 and 1900 hr and were distributed relatively evenly throughout the day (Table 8). Due to time constraints, these 2 hr observations were occasionally begun somewhat earlier or later than their scheduled time. However, no observation was allowed to begin more than 15 minutes before or after the listed time. In addition, for any given animal, the total deviation from the standard starting time for all seven trials was not allowed to exceed 30 minutes, so all subjects were observed within 95% of the same time of the day.

(B) Using the same camera set-up as above, animals were observed for 10 min trials, during which posture and site changes were recorded. Isolate animals were observed seven times while paired animals were observed 14 times (seven with their partner in the same compartment and seven when their partner was in a separate compartment). These observations took place between 1300 and 1600 hr (Table 8).

Table 8. Distribution of observations throughout the day for *Anolis carolinensis* males.

Variables Recorded	Time Period of Observations	Number of Observations During Period	Length of Observations
Number of Compartment Changes Timing of Changes	0900-1100	1	2 hr
	1000-1200	1	2 hr
	1200-1400	1	2 hr
	1330-1530	1	2 hr
	1500-1700	1	2 hr
	1600-1800	1	2 hr
	1700-1900	1	2 hr
Posture Changes Site Changes	1300-1330	2*	10 min
	1430-1500	3*	10 min
	1530-1600	2*	10 min
Color Posture Site Selection Activity	0900-1100	6*	Instantaneous
	1100-1300	5*	Instantaneous
	1300-1500	5*	Instantaneous
	1500-1700	5*	Instantaneous
	1700-1900	4*	Instantaneous

* Paired animals were actually observed "twice" in these categories, once when their partner was present and once when he was absent. Therefore, a subordinate or dominant male would have been observed a total of *four* times from 1300 to 1330 while an isolate male would have been observed two times.

INSTANTANEOUS SCANS

(C) Animals were briefly scanned and their body color, posture, site selection and activity levels were recorded using an ordinal scale (Fig. 2). Isolates were scanned 25 times. Paired animals were scanned 50 times, half when their partner was present in the same compartment and half when their partner was absent. These observations took place between 0900 and 1900 hr and were distributed relatively evenly throughout the day (Table 8).

Depending on the length of a particular trial, the observations were spread out over the course of 4 to 17 days. To reduce the possibility that a lizard being observed on an "off" day would bias the results, only one, 2 hr observation was allowed on any given day for an animal. For the same reason, only one, 10 min observation and no more than three instantaneous scans were allowed for any testing condition (i.e. paired with partner absent vs. paired with partner present). The variation in the length of the trials was largely due to the difficulties of observing paired animals with or without their partners present. First, the lizards had to move into the desired testing condition on their own without outside manipulation. Second, since the animals were not restricted from moving during the course of the observations, trials frequently had to be terminated when one of the animals changed compartments (and therefore the testing condition). In any case, no more than one day was ever allowed to pass without animals being observed and data taken.

Color Index: An ordinal scale of body colors observed.

1. All visible pigmented body surfaces a light to moderate green.
2. Part green/Part brown.
3. All visible pigmented body surfaces a light to moderate brown.
4. More than 50% of the body surface is dark brown.
5. Dark brown with an eyespot (ES). A black spot near the posterior margin of the orbit.
6. All visible pigmented body surfaces moderate to dark green with an eyespot.
7. Body color is blotchy, irregularly pigmented dark green and dark brown, with eyespot.

Posture Index: An ordinal scale of body postures observed.

1. Head and Body Up, High ("Alert")
2. Head and Anterior Body Up, Moderate
3. Head Slightly Elevated
4. Head Down on Substrate
5. Head Down, Rear Legs Back ("Cryptic")

Site Selection: An ordinal scale of perching sites observed.

1. Top of Perch.
2. Upper half of Perch
3. Lower half of Perch
4. On the Substrate
5. Covert Perching; Hiding; Squirreled around the perch or behind the water bottle; Out of the line of sight for the other lizard.
6. Burrowed into the substrate; Frequently with only the head above the surface.

Activity Index: An ordinal scale of the various activities seen by animals from most active (1) to least active (6).

1. Site Change; Animal moves from location to another.
2. Head Scan.
3. Posture Change; Occurs when an animal's head remains stationary but his body shifts its position.
4. Eye Movement.
5. Eyes Open (but no movement).
6. Eyes Closed.

Figure 2: Scoring protocol for body color, posture, site selection and general activity levels in green anole lizards (*Anolis carolinensis*).

Adapted from Greenberg, N. and D. Crews. 1990. Endocrine and behavioral responses to aggression and social dominance in the green anole lizard, *Anolis carolinensis*. *Gen. Comp. Endocrinol.*, 77:246-255.

Definition of Variables

Body Color: This refers to the color of the animal at a particular moment in time.

Although not a behavior per se, it was included in this study because it is considered a noninvasive measure of stress levels in *A. carolinensis* (Greenberg et al. 1984). Lower scores indicate greener, less stressed animals (Fig. 2).

Posture: This is a measure of an animal's level of "arousal" The lower the score, the more alert the animal is considered to be (Fig. 2).

Site Selection: This variable measures the relative perch height that an animal occupies within the testing chamber. Lower scores reflect higher perch sites (Fig. 2).

Activity Levels (ACT): This variable is a general measure of an animal's overall activity level. It measures "small scale" movements such as a change in the posture of an animal or moving from one location to another (often within the same compartment). Low ACT scores indicate high levels of activity (Fig. 2). (Please note that, throughout the rest of this thesis, "ACT" will be used to refer to the ordinal rank score for a particular animal or group of animals. The term "activity" will be used as a qualitative description of the behavior of an animal or a group of animals.

Posture Change Rates (PCR): This variable is a component of ACT. It is concerned with adjustments in body posture not associated with locomotion (mainly head scans). It is determined using continuous data recording rather than an instantaneous scan.

Site Change Rates (SCR): This variable is a component of ACT. It involves displacement of the body's center of gravity. It is determined through continuous data recording.

Total Compartment Changes (TCC) or Patrolling: This variable is a component of ACT and is related to SCR. However, it is a measure of "large scale" movements where animals move from one compartment into a different one.

Statistical Analysis

Each animal served as his own control. An examination of the raw data showed that there was no time effect, either from the hour of the day or the length into the study (Friedman Two-Way Anova, NS). Consequently, observations for a particular animal were averaged to provide a single score for each variable. When examining the data for dominants and subordinates, observations made while the animals were alone in a compartment were analyzed separately from observations made when the other animals were with them. Comparisons of paired data were made using the Wilcoxon Matched Pairs Signed Rank Test. The chi-square test was used to analyze the patterns

of movements into empty and occupied compartments as well as where the animals spent their time within the testing chamber. Analyses were carried out using SPSS for Windows.

The time spent in each compartment was analysed using a two-way ANOVA with group (control and treatment) and time (before and after) as the independent variables. However, the data were not normally distributed and the residuals were not normally distributed. Therefore, the data were transformed using a square root transformation. The transformed data were then analysed using a two-way ANOVA. The results of the ANOVA are presented in Table 1. The ANOVA showed a significant main effect of time ($F_{1,18} = 10.0, p < 0.01$) and a significant interaction effect of group and time ($F_{1,18} = 10.0, p < 0.01$). The post-hoc analysis showed that the treatment group spent significantly more time in the occupied compartments after the treatment than the control group. There was no significant difference in the time spent in the empty compartments between the two groups.

Effect of treatment on the number of movements

The number of movements made by the rats was analysed using a two-way ANOVA with group (control and treatment) and time (before and after) as the independent variables. The data were not normally distributed and the residuals were not normally distributed. Therefore, the data were transformed using a square root transformation. The transformed data were then analysed using a two-way ANOVA. The results of the ANOVA are presented in Table 2. The ANOVA showed a significant main effect of time ($F_{1,18} = 10.0, p < 0.01$) and a significant interaction effect of group and time ($F_{1,18} = 10.0, p < 0.01$). The post-hoc analysis showed that the treatment group made significantly more movements after the treatment than the control group. There was no significant difference in the number of movements between the two groups before the treatment.

CHAPTER III

RESULTS

The terms “pre-dominant” and “pre-subordinate” are used through the rest of this paper for ease of discussion. However, as stated earlier, dominance is an emergent property and can only exist when there are two animals present. It describes the relationship rather than the animals. The term pre-dominant or pre-subordinate is simply used to identify the way that an animal behaved when it was not paired with another individual.

Pre-Dominants vs. Pre-Subordinates

The total number of compartment changes were significantly higher ($P < 0.05$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) in the pre-dominant members of the pairs ($\bar{x} = 40.0$) than they were in the pre-subordinate members ($\bar{x} = 29.89$) (Fig. 3). In seven out of nine pairs, the animal that would become the dominant had a higher rate of movements between compartments as an isolate than did his partner. Other than TCC, pre-dominants and pre-subordinates did not vary significantly for any variables including size (Wilcoxon Matched Pairs Signed Rank Test, NS). In addition, TCC was not correlated with any of the other variables (Spearman's Rank Correlation, NS).

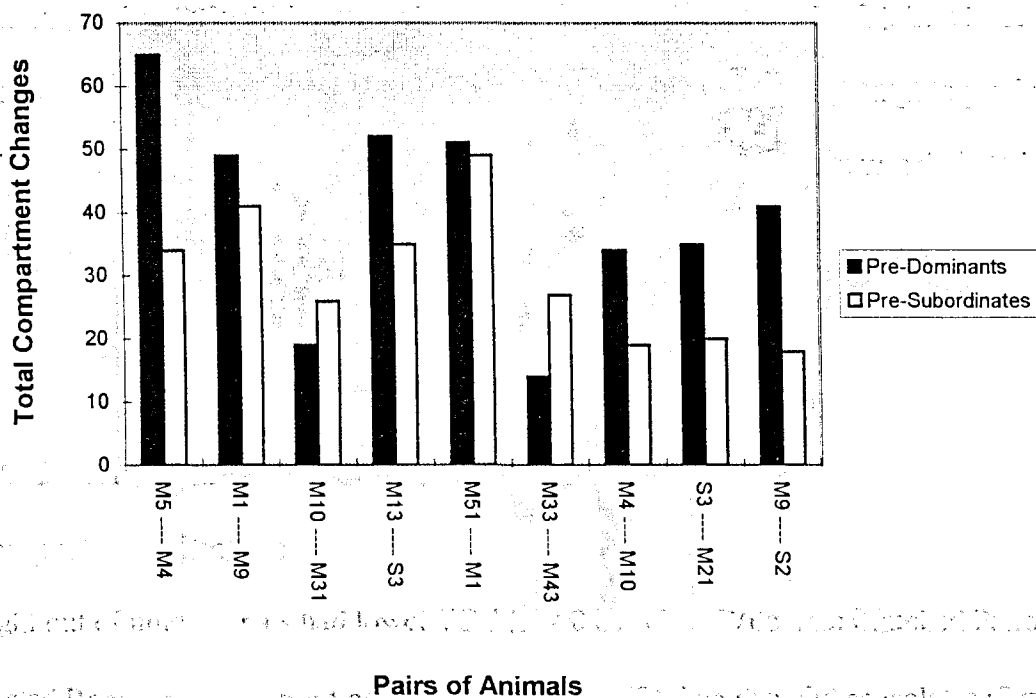


Figure 3. TCC made by each member of a dominant/subordinate pair of *Anolis carolinensis* when the lizards were alone (ISOLATES) in the testing chamber. The animals that became dominants are listed first for each pair.

During the course of the study, the lizard with the highest number of compartment changes as an isolate, M5, was paired with four other males in an effort to create a pairing where he would be a subordinate animal. In each case, he defeated his opponent and took the dominant role even when he was matched with animals with masses over 1 g greater than his own (a difference in body mass of 1 g represents approximately a 20% difference in body mass between the two animals). The least active animal, S2, was also paired with several other animals in an attempt to produce a situation where he was the dominant male. In each case, though, he was defeated by his opponent.

Isolates vs. Paired Animals

SUBORDINATES

Compartment Changes

Eight out of nine animals had lower TCC ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) as subordinate animals ($\bar{x} = 28.89$) than they did as isolates ($\bar{x} = 14.78$) (Fig. 4).

Isolates Vs. Paired Animals (Partner Present or Absent)

A summary of scores for lizards that became subordinates can be found in Table 9 and Table 10.

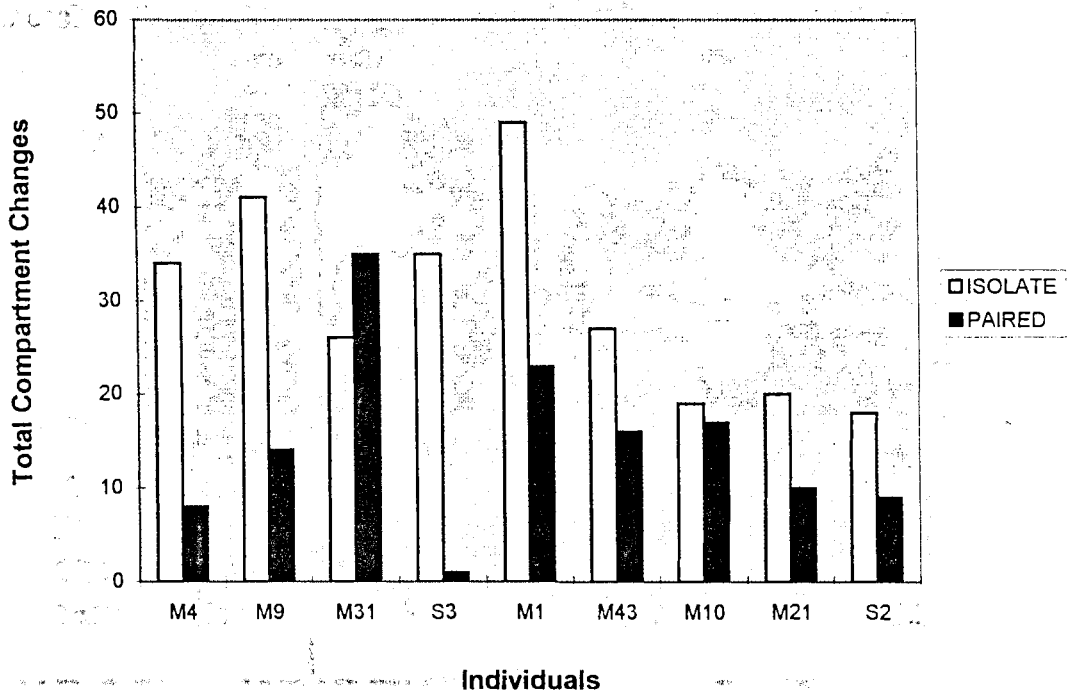


Figure 4. TCC made by *Anolis carolinensis* males that became subordinates. Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males.

Table 9. Average rank scores for color, posture, site selection and general activity for *Anolis carolinensis* males that became subordinates. Scores were calculated using ordinal ranks to classify each variable (see Fig. 2). Each animal was observed 25 times for each testing condition.

Variable	Testing Condition		
	Isolate	Paired Dominant Absent	Paired Dominant Present
Color Index	1.83	3.34	3.68
Posture Index	2.09	2.30	3.27
Site Selection	2.59	2.56	3.42
Activity Index	3.09	2.78	4.23

N=9
 See text for explanation of any differences between testing conditions.

Table 10. Average rates of posture and site changes (per minute) for *Anolis carolinensis* males that became subordinates. Each animal was observed seven times for each testing condition for a total of 70 minutes.

Variable	Testing Condition		
	Isolate	Paired Dominant Absent	Paired Dominant Present
Posture Changes	9.27	14.53	1.02
Site Changes	0.68	1.10	0.10

N=9

See text for explanation of any differences between testing conditions.

Body Color

As reported in other studies (Greenberg et al. 1984; Greenberg and Crews 1990), subordinates were darker in color than they had been as isolates. This was true whether they were in the same compartment as the dominant animal or whether they were alone ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) (Fig. 5 and Table 9). Subordinates were also significantly darker in color when they were in the presence of the dominant males than when they were alone ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test).

Posture and Site Selection

Subordinates had higher posture indices (indicating more submissive body postures, see Fig. 2) than they did as isolates, but only when they were in the presence of the dominant animal ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) (Fig. 6 and Table 9). When subordinates were alone in a compartment, their postures were unchanged from their baseline, isolate levels. The same held true for relative perch height selections. Subordinates adopted lower perch sites but only when they were near the dominant ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) (Fig. 7 and Table 9). Otherwise, there was no change from isolate levels.

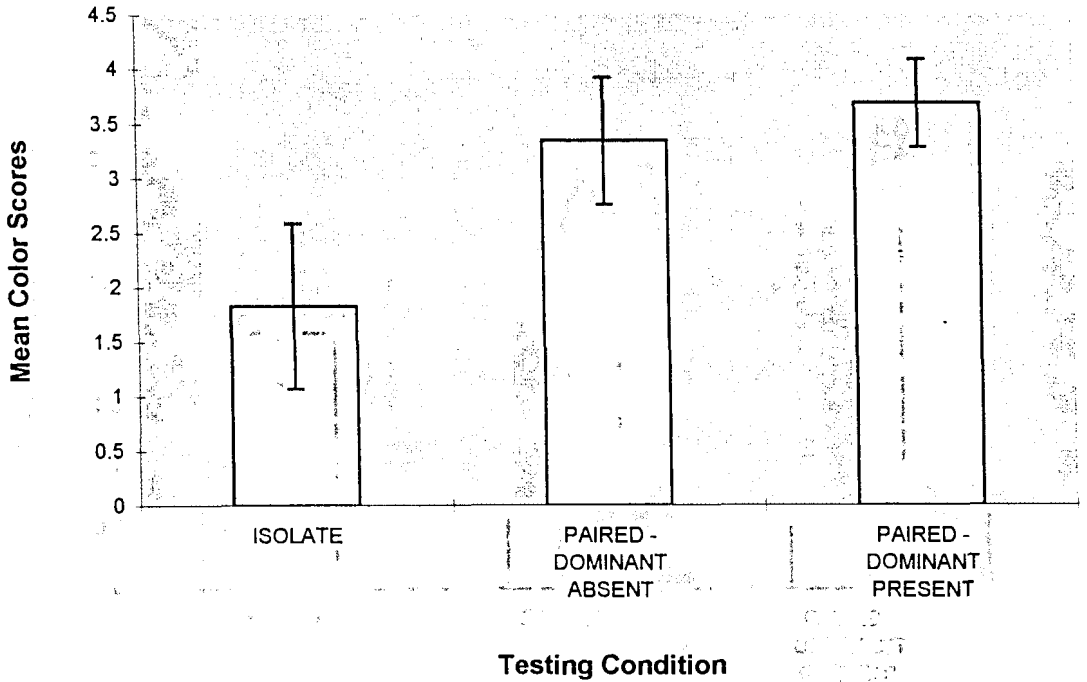


Figure 5. Changes in body color for *Anolis carolinensis* males that became subordinates. Larger numbers indicate darker colors (see Fig. 2). Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males. Mean and one standard deviation are indicated (N=9).

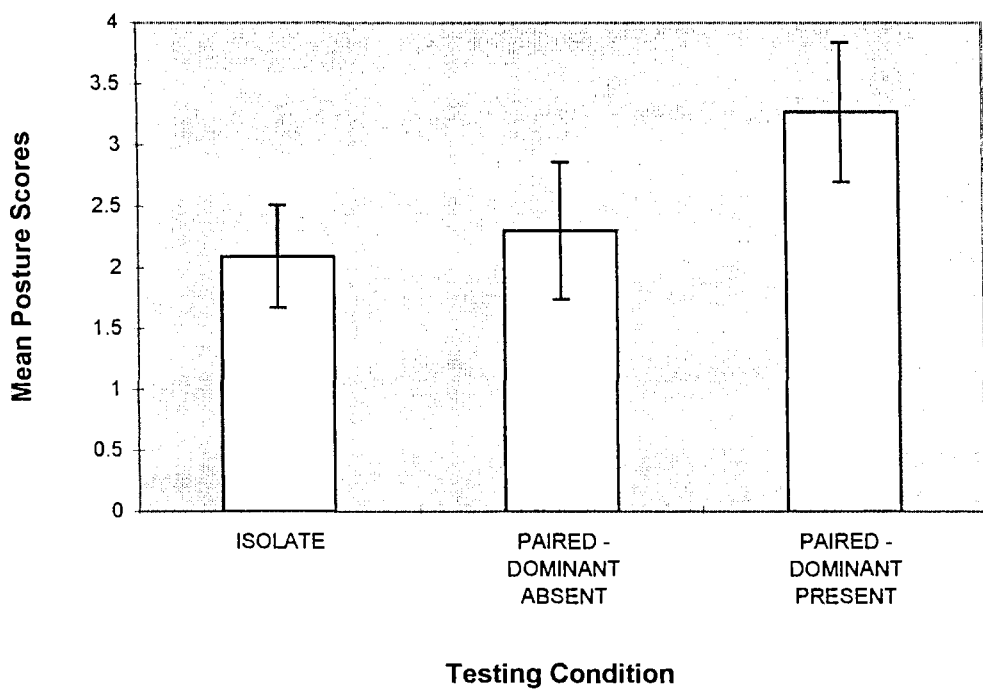


Figure 6. Changes in posture for *Anolis carolinensis* males that became subordinates. Higher scores reflect more submissive postures (See Fig. 2). Mean and one standard deviation are indicated (N=9).

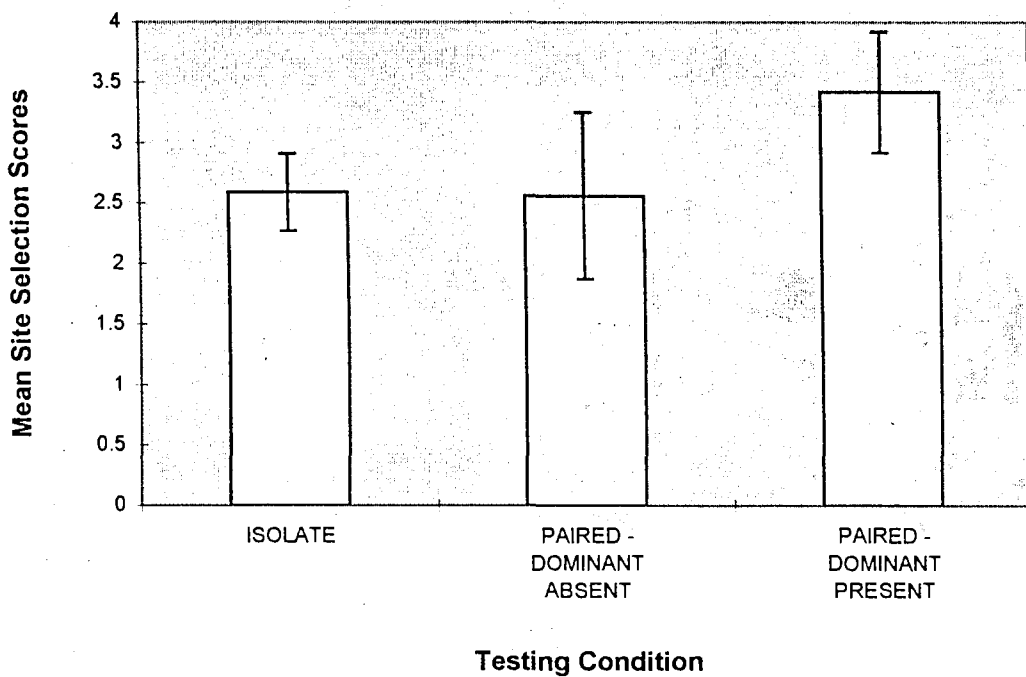


Figure 7. Changes in site selection for *Anolis carolinensis* males that became subordinates. Higher scores reflect lower, more covert perch sites (See Fig. 2). Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males. Mean and one standard deviation are indicated (N=9).

General Activity

Subordinates that were in the same compartment with dominants were significantly less active than they were as isolates ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) (Fig. 8 and Table 9). However, subordinates that were in separate compartments from dominants were significantly more active than they had been as isolates ($P < 0.05$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test).

Posture Change Rates

Subordinates had significantly higher PCR ($P < 0.05$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) when the dominant was absent ($\bar{x}=14.53$ changes/min) than they had as isolates ($\bar{x}=9.27$ changes/min) (Fig. 9 and Table 10). They also showed significantly decreased rates ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) when the dominant animals was present in the same compartment ($\bar{x}=1.02$ changes/min).

Site Change Rates

The pattern of SCR followed that the same one as the PCR scores (Fig. 10 and Table 10). Subordinates showed increased SCR ($P = 0.06$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) when the dominant was absent ($\bar{x}=1.1$ changes/min) compared to when they had been isolates ($\bar{x}=0.68$ changes/min). They also showed significantly

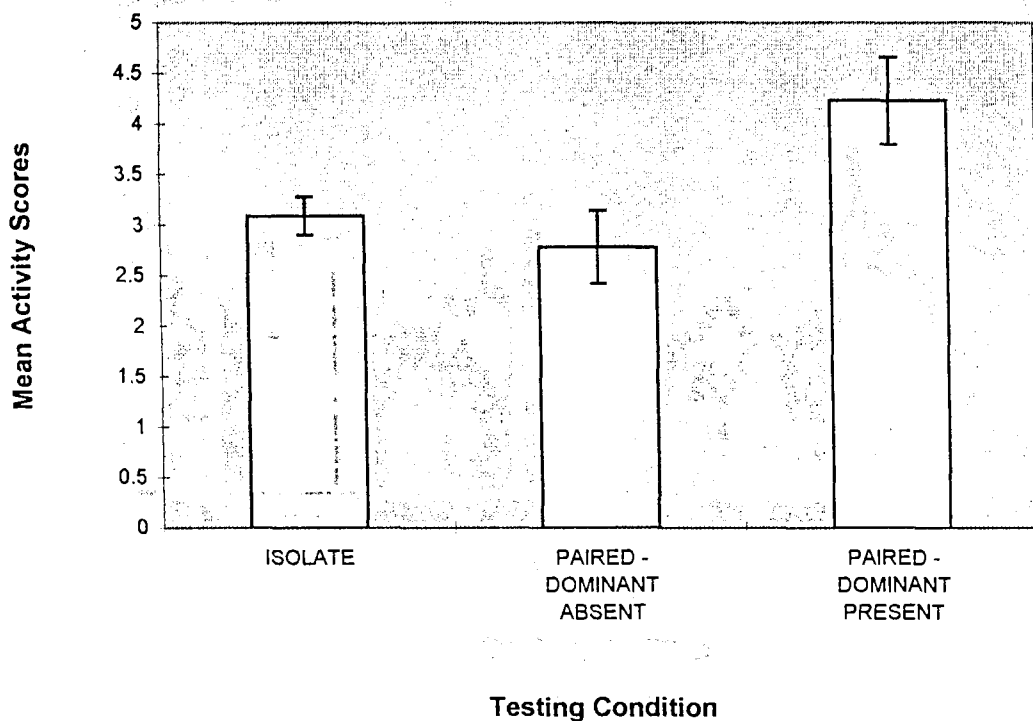


Figure 8. Changes in ACT for *Anolis carolinensis* males that became subordinates. Higher scores reflect lower levels of activity (See Fig. 2). Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males. Mean and one standard deviation are indicated (N=9).

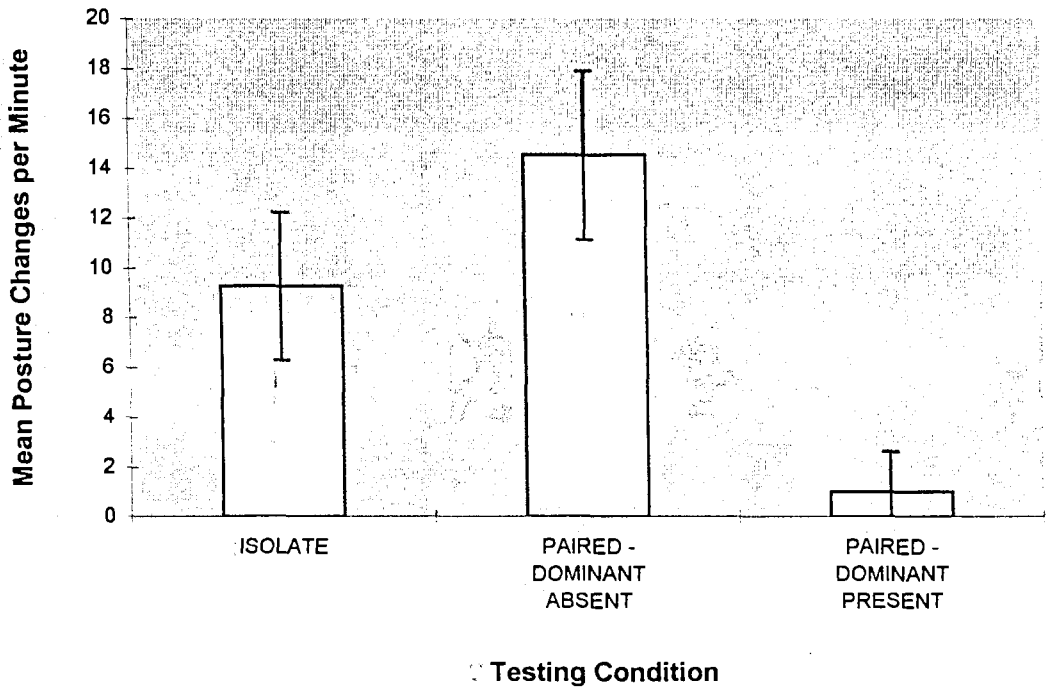


Figure 9. Changes in PCR for *Anolis carolinensis* males that became subordinates. Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with another male. Mean and one standard deviation are indicated (N=9).

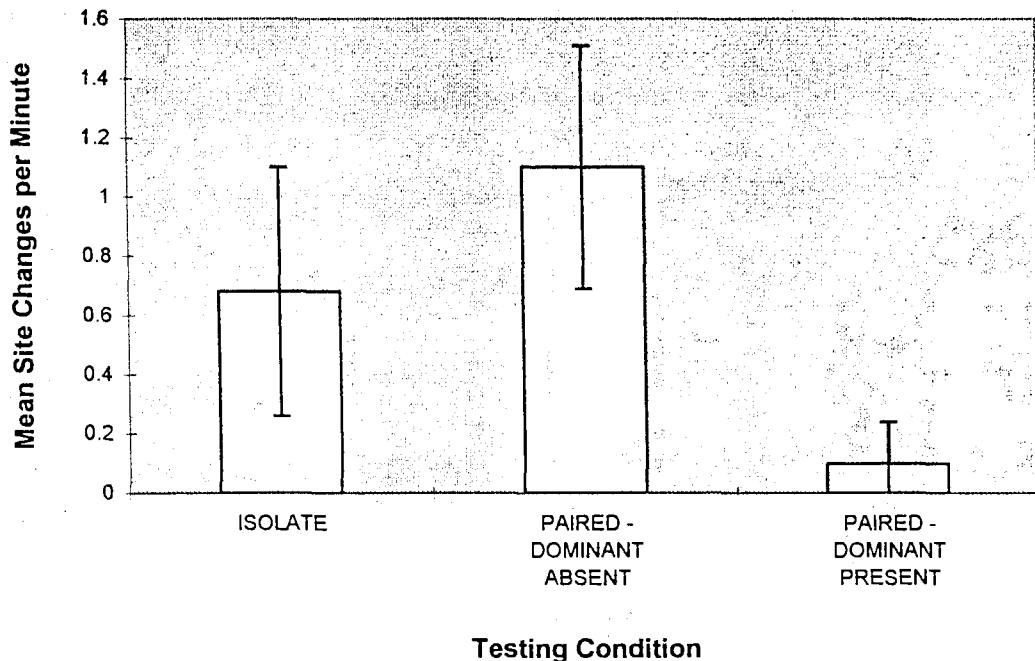


Figure 10. Changes in SCR for *Anolis carolinensis* males that became subordinates. Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males. Mean and one standard deviation are indicated (N=9).

decreased rates ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) when the dominant animals was present in the same compartment ($\bar{x}=0.10$ changes/min).

DOMINANTS

Compartment Changes

Nine out of nine animals had higher TCC ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) as dominant animals ($\bar{x} = 58.67$) than they did as isolates ($\bar{x} = 40$) (Fig. 11).

Isolates Vs. Paired Animals (Partner Present or Absent)

A summary of scores for lizards that became dominants can be found in Table 11 and Table 12.

Body Color, Posture, Site Selection and General Activity

Dominants showed no changes from their isolate levels in any of these categories, regardless of whether or not they were in the same compartment as the subordinate (Table 11) (Wilcoxon Matched Pairs Signed Rank Test, NS).

Posture Change Rates

Dominant animals showed significantly lower PCR ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) from isolate levels ($\bar{x} = 9.14$ changes/min). This was

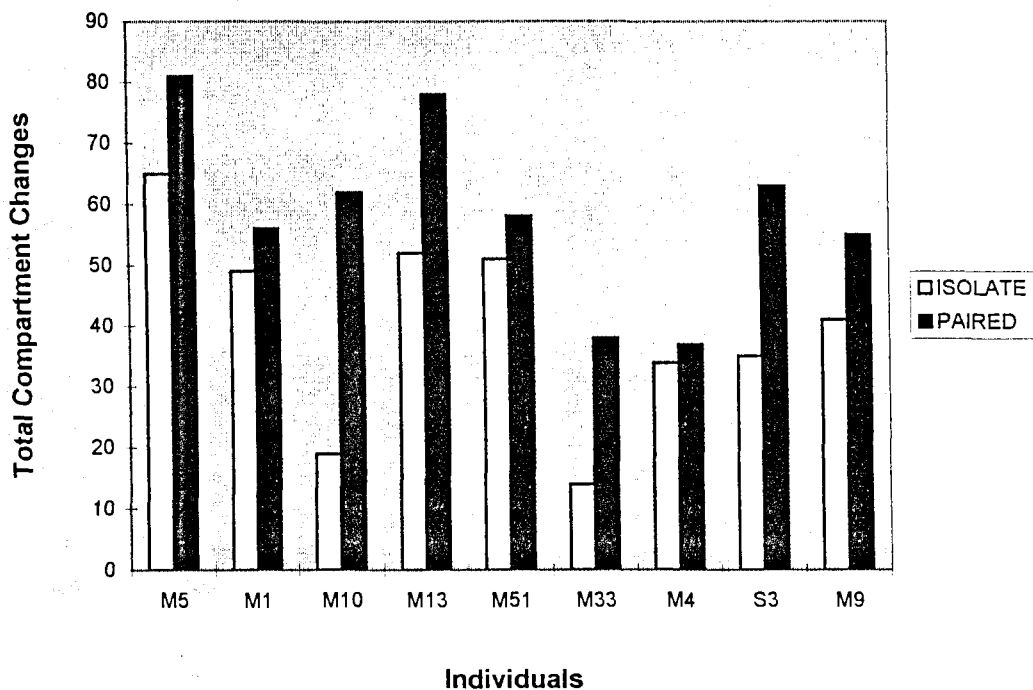


Figure 11. TCC made by *Anolis carolinensis* males that became dominants. Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males.

Table 11. Average rank scores for color, posture, site selection and general activity for *Anolis carolinensis* males that became dominants. Scores were calculated using ordinal ranks to classify each variable (See Fig. 2). Each animal was observed 25 times for each testing condition.

Variable	Testing Condition		
	Isolate	Paired Subordinate Absent	Paired Subordinate Present
Color	2.10	2.14	2.22
Posture	2.59	2.47	2.44
Site Selection	2.11	2.20	2.10
Activity	2.92	2.92	3.01

N=9

There were no significant differences among any of the testing conditions for any of these variables.

Table 12. Average rates of posture and site changes (per minute) for *Anolis carolinensis* males that became dominants. Each animal was observed seven times for each testing condition for a total of 70 minutes.

Variable	Testing Condition		
	Isolate	Paired Subordinate Absent	Paired Subordinate Present
Posture Changes	9.14	7.59	4.61
Site Changes	0.76	0.46	0.23

N=9

See text for explanation of any differences between testing conditions

true whether they were in the same compartment with the subordinate ($\bar{x} = 4.61$ changes/min) or if the subordinate lizard was absent ($\bar{x} = 7.59$ changes/min) (Fig. 12 and Table 12). In addition, the PCR of dominants was significantly lower ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) in the presence of the subordinates than it was in their absence.

Site Change Rates

Dominant animals showed significantly lower SCR ($P < 0.05$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) from isolate levels ($\bar{x} = 0.76$ changes/min). This was true whether they were in the same compartment with the subordinate ($\bar{x} = 0.23$ changes/min) or if the subordinate lizard was absent ($\bar{x} = 0.46$ changes/min) (Fig. 13 and Table 12). In addition, the SCR of dominants was significantly lower ($P < 0.01$, $N=9$, Wilcoxon Matched Pairs Signed Rank Test) in the presence of the subordinates than in their absence.

Location of Animals

Isolates and dominants tended to spend equal amounts of time in all three compartments of the testing chamber ($X^2=16.7$, 2 df, NS for isolates; $X^2=16.7$, 2 df, NS for dominants) (Table 13). Subordinates, however, showed a strong bias against the center compartment ($X^2=16.7$, 2 df, $P<0.01$).

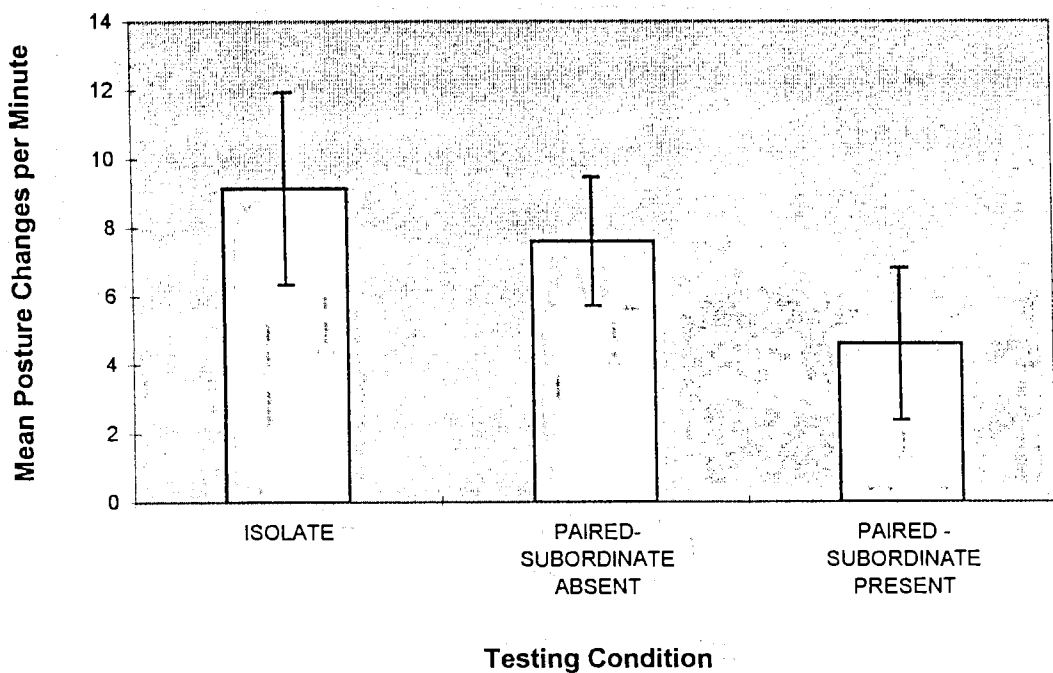


Figure 12. Changes in PCR for *Anolis carolinensis* males that became dominants. Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males. Mean and one standard deviation are indicated (N=9).

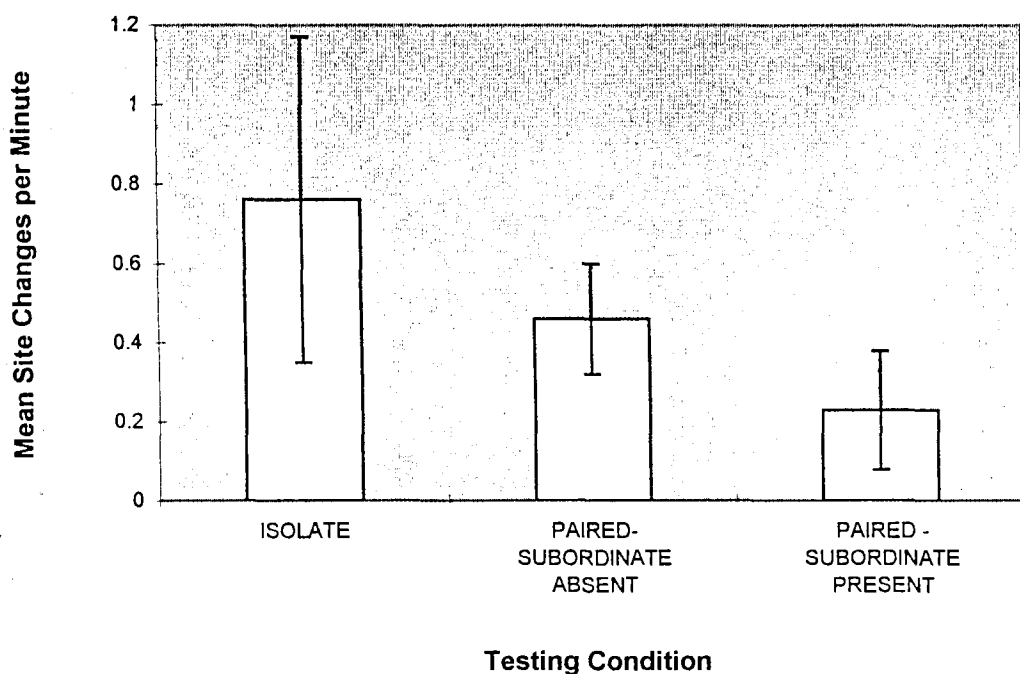


Figure 13. Changes in SCR for *Anolis carolinensis* males that became dominants. Scores are shown for before (ISOLATE) and after (PAIRED) lizards were placed with other males. Mean and one standard deviation are indicated (N=9).

Table 13. Percentage of time *Anolis carolinensis* males spent in each of the compartments of the testing chambers.

Group	Percentage of Time Spent in Each Compartment		
	Left	Center	Right
Isolates	36.66	31.03	32.31
Dominants	33.03	41.52	25.45
Subordinates	44.87	14.21	40.93
Dominants and Subordinates Together*	15.99	6.88	12.88

N=9

* The category "Dominants and Subordinates Together" refers to those occasions when both members of a pair were present in the same compartment at the same time.

Pattern of Movements

The movement patterns of dominants and subordinates through the testing chamber were quite different (Fig. 14 and Table 14). Entering an occupied compartment accounted for 38.8% of all dominant moves but subordinates only moved into occupied compartments 7.5% of the time. In addition, over half of all subordinate movements involved leaving an occupied compartment (53.4%). Dominant animals, however, only moved out of occupied compartments 26.5% of the time.

Subordinates changed compartments a total of 133 times during the trials, 52 of which involved moving from one empty compartment to another. Of those 52 changes, however, 20 of them (38.5%) occurred less than two minutes after they had walked out of an occupied compartment. These changes were essentially "continuous movements," ones in which the animal essentially walked from one end compartment to the other without ever stopping. Dominant animals only showed these continuous movements in 17 out of the 181 moves (9.4%) that they made from one empty compartment to another. If these continuous movements are included in the Occupied to Empty category, then subordinates moved out of occupied compartments 68.4% of the time, while dominants moved out 29.8% of the time.

If the animals were moving through the compartments randomly, then we would expect for the moves to be divided equally between the three possible categories (Occupied to Empty, Empty to Empty, Empty to Occupied). However, a chi square

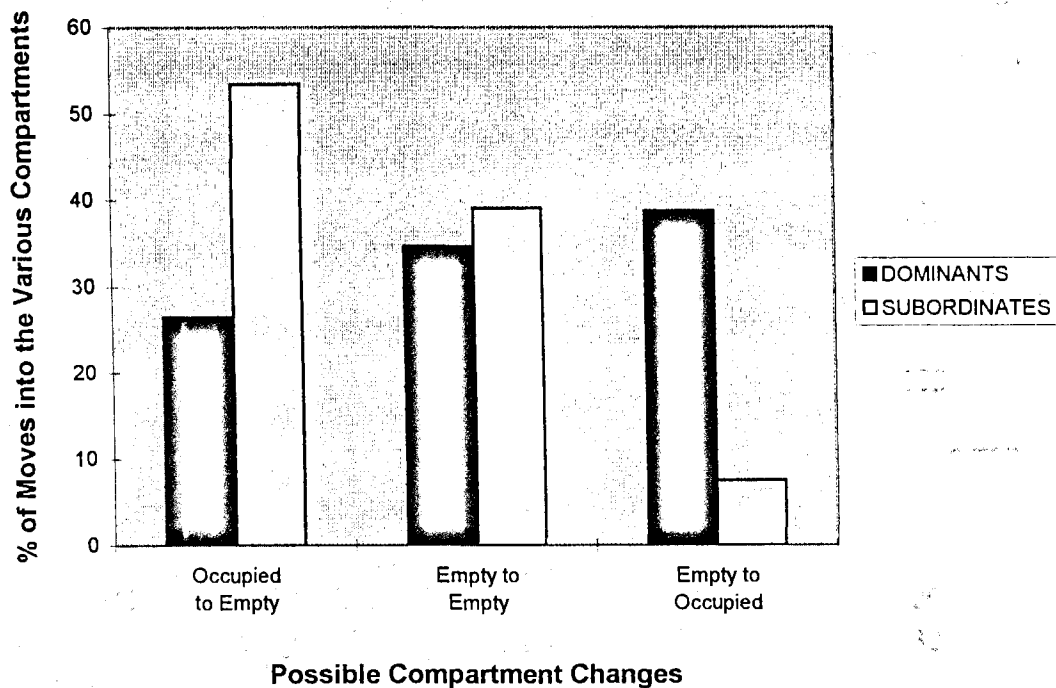


Figure 14. Comparison of the movement patterns of dominant and subordinate *Anolis carolinensis* males.

Table 14. Breakdown of the compartment changes made by dominant and subordinate *Anolis carolinensis* males. The category "Moves < 2 min after leaving Occupied" represents those times when an animal left an (occupied) end compartment and moved through the center without stopping to reach the opposite end compartment. These can be considered an "continuation" of the original "Occupied to Empty" compartment change.

	Dominants	Subordinates
ALL CHANGES		
Empty to Empty	181	52
Empty to Occupied	202	10
Occupied to Empty	138	71
Total	521	133
EMPTY TO EMPTY ONLY		
Moves < 2 min after leaving Occupied	17	20
All other Empty to Empty	164	32
ALL CHANGES With Continuous* Movements Included as Occupied to Empty		
Empty to Empty	164	32
Empty to Occupied	202	10
Occupied to Empty	155	91

* Moves < 2 min after leaving Occupied = Continuous Movements

analysis indicates that the movement patterns of both dominants and subordinates varied significantly from what would be expected by random chance ($X^2=11.85$, 2 df, $P < 0.01$ for dominants; $X^2=44.9$, 2 df, $P < 0.001$ for subordinates). Subordinates showed a strong tendency to leave occupied compartments while dominants were only half as likely to do so. Subordinates also avoided entering occupied compartments while dominants entered occupied compartments at a slightly higher than expected rate (38.8% vs. 33.3%).

CHAPTER IV

DISCUSSION

Pre-Existing Differences in the Behaviors of Unpaired (Isolate) Animals

Animals that did the most patrolling as isolates (had the highest TCC) repeatedly defeated animals that moved around less. There were two instances where the more active isolate animal was not the dominant one after pairing. The one thing these pairings have in common is that these were also the only times when there was a considerable difference in the sizes of the animals. In both cases, the animal that became dominant was over 1 g (approximately 20%) heavier than the subordinate was. In the other seven pairings, the dominant and subordinate animals had masses within 0.5 g of each other.

This same phenomenon was seen in the pilot study for this research. In that experiment, three out of four times, the animal that did more patrolling as an isolate animal defeated his opponent (see Table 1). The one exception to this rule again involved a pair of animals in which the dominant animal was much larger than his opponent. These results suggest that the size of the lizards may influence the outcome

of the fights, but only when the difference in the animals' sizes is relatively large.

When animals are reasonably close in size, however, the amount of patrolling that an animal does is an accurate indicator of which animals are likely to win dyadic encounters.

Despite the fact that there does seem to be a relationship between the amount of patrolling an animal does as an isolate and his ability to win fights with conspecifics, there is no reason to believe that this is a causal relationship. More likely it is due to some third, unknown variable that influences them both. One possibility would be the levels of testosterone in the animals. Moore (1987) and Moore and Marler (1987) reported that testosterone levels positively affected movement rates (patrolling) and aggressive and territorial behaviors in free-living *Sceloporus*. DeNardo and Sinervo (1994) found that implanting *Uta stansburiana* (Phrynosomatidae) with testosterone increased their activity and home range sizes.

Testosterone has been shown repeatedly to influence aggression in lizard species.

Reductions in levels inhibit aggression (Moore 1987; DeNardo and Licht 1993) and increases result in elevated levels of aggression (Fox 1983; Moore 1986; Moore and Marler 1987). Androgen has also been demonstrated to affect aggressive behavior in *A. carolinensis* (Greenberg et al. 1984, Greenberg and Crews 1990). It is possible that certain animals simply have higher levels of circulating androgen, giving them an advantage over conspecifics. It is also possible that there are no differences in the

levels of testosterone per se but rather there are differences in the sensitivity of the receptors to circulating hormones.

One simple method for determining what influences, if any, that testosterone has on the amount of patrolling that *A. carolinensis* does would be to use castrates and implanted animals. If testosterone actually does affect patrolling in some way, then we would expect castrates to move around less after surgery and implanted animals to move around more. One problem that would also need to be addressed is the issue of corticosterone. This hormone has been observed to inhibit aggression in some species of lizards (Tokarz 1987; DeNardo and Licht 1993). Corticosterone not only reduces the actual levels of testosterone (Tokarz 1987; DeNardo and Licht 1993) but can also inhibit aggression even when testosterone levels are kept artificially high (DeNardo and Licht 1993). DeNardo and Sinervo (1994) found that animals implanted with corticosterone showed a reduction in both activity and in home range size, even when the animals were implanted with testosterone as well. On the other hand, Greenberg and Crews (1990) found that animals can become subordinates and show lowered aggression even when corticosterone levels remain relatively unchanged, so it is likely that whatever the effects of this hormone are, they are multiple and complex.

Finally, it should be noted that it is not simply activity that is related to the winning of fights but rather one specific form of activity: TCC or patrolling. There were no differences between pre-dominants and pre-subordinate for the other three variables

used to describe the activity levels of the animals: SCR, PCR and ACT. This suggests that the mechanisms by which these behaviors are controlled differ from those that control the amount of patrolling an animal does.

The Effects of Social Dominance on a Green Anole

ACTIVITY LEVELS

In every trial but one, subordinates changed compartments less frequently than they did as isolate animals. The reason for this exception is likely attributable to the fact that this subordinate was paired with a particularly aggressive dominant male. This dominant (M10) engaged in numerous aggressive displays and on several occasions rushed the subordinate (M31) as if to attack. On these occasions, the subordinate tended to quickly leave the compartment and moved as far away from the dominant male as possible, who invariably found him and chased him again. (M10 showed the most dramatic increase in TCC among dominants, showing over three times more changes as a dominant than he did as an isolate.)

The decrease in TCC seen in the other subordinates and the increase seen among dominants may be due to the issues of testosterone (and corticosterone) addressed in the previous section. Greenberg and Crews (1990) found that losers of fights had lower levels of circulating androgen but that corticosterone levels were not significantly affected. However, as mentioned earlier, they also found that, although winners had elevated levels of androgen one hour after a fight, the levels had returned

to near control levels by one week. Dominant males in this study showed increased rates of compartment changes even after ten days had passed, however, so it is quite possible that something other than testosterone was driving the increase in patrolling that was seen.

Whether or not these patterns were caused by testosterone or some other hormone, they have been seen in other studies. Raab et al. (1986) found that dominant rats increased their levels of exploratory behavior in open field tests, while subordinates showed decreased levels. Numerous experiments (Kahn 1951; Raab et al. 1986; Scholtens et al. 1988; Williams and Lierle 1988; Kudryavtseva et al. 1991) have reported that defeat by conspecifics can cause long lasting inhibition of aggression, increased expression of submissive behavior, freezing and decreased motor activity or exploratory behavior in rodents.

The decrease in general activity, PCR, and SCR among the subordinate animals when they were in the presence of the dominant males was reasonable, as any kind of movement by subordinates often elicited aggressive responses from the dominants. What is interesting is that, when dominants were not present, subordinate activity levels were actually higher than their baseline, isolate levels. One possible explanation for this may be that subordinates were looking for the dominant males. An animal that failed to see the dominant enter the compartment would certainly be more vulnerable to attack than would one who saw the dominant and could then hide or act submissive.

When a subordinate was alone in an end compartment, he tended to remain oriented towards the door, again perhaps in an effort to watch for the dominant male (pers. obs.).

The fact that dominant males showed depressed levels of PCR and SCR, relative to their isolate levels, in the absence of the subordinate is not as easily understood and was certainly not expected. It was particularly surprising that the rates decreased even further when they were in the presence of the subordinate. One possible explanation for the latter result could be that dominants are attempting to "conserve" energy in case a possible confrontation arises. It also may simply be the case that they tended to orient towards subordinates when they could see them and rarely looked away for more than a few seconds when they were present. In many cases, the movements of the dominant males appeared to be much slower and more "precise" when they were in the same compartment as the other animal (pers. obs.). Since PCR recorded the animals looking around the cages, giving the dominant something to focus his attention on could lead to a reduction in the rate at which his posture changed.

The various activity measures for dominants seem to contradict each other in certain ways. First, although SCR decreased, TCC increased. This may be because a site change does not record the distance that an animal traveled but simply the fact that its location changed. A continuous movement from one compartment to another would only count as one site change. Dominants changed compartments more frequently than

they did as isolates but within a particular compartment, they tended to remain relatively stationary.

The second seeming contradiction is that the ACT scores for dominants remained essentially unchanged, yet they showed decreased PCR and SCR. One possible explanation for this may be a result of the manner in which the data were taken. When determining whether a posture or site change had occurred, I was consistently “generous” in deciding that a change had taken place. Small differences that might not have been considered enough to constitute a change in posture to another researcher were regularly scored as such during my observations. Thus, the rates documented were relatively high compared to what another person might record. Since I was similarly discriminating with all animals in all conditions, there is no problem with the quality of the data collected. However, the ACT score did not reflect the number of posture changes during the time it took to scan an animal but simply that such a change had occurred. Since I counted even small alterations as changes in posture, it would have been easy for an animal to be scored as making at least one posture change during a scan.

COLOR, POSTURE AND SITE SELECTION

Body color in green anoles is known to be under the control of circulating hormones associated with stress physiology (Greenberg and Crews 1983). Hormonal control is generally associated with slower, more long-term shifts in behavior. Unlike several

other variables observed, subordinates were darker in color than they had been as isolates whether they were in the same compartments as the dominant males or not. This is consistent with the idea of a mechanism that can not simply be turned on and off at will. Even though they were darker in color when the dominant animals were present, they still did not return to baseline isolate levels when the dominants were absent.

The posture and the site selection of the subordinates, however, only differed from isolate levels when they were in the same compartment as the dominant animals. When they were alone, they behaved essentially the same as they had when they were isolate animals. Greenberg and Crews (1990) suggested that perch height selection might be hormonally mediated in a similar manner to color, an idea supported by Greenberg and Lumsden (1990) who found that castrates had lower perch-site selections. The data collected in this study, however, do not seem to support that idea. Although a hormonal influence cannot be discounted, it would seem likely that there is a separate method of control, perhaps neural, that governs perch height selection (and posture) in these animals and allows the subordinates to make rapid changes in their behavior when the dominant males are not present.

Whether the altered body color of subordinates is adaptive is unclear. However, lower perch heights and postures that are more submissive are most likely an attempt by subordinates to reduce aggression from the dominant males. Animals were seen to

adopt lower perch sites and postures in response to displays from dominant males. In many cases, dominant males ended their displays soon after the subordinates assumed the more submissive behaviors (pers. obs.). In addition, subordinates frequently moved to lower perch sites and performed more submissive postures *before* dominants had the opportunity to display. In many of these instances, dominants took possession of the abandoned perch sites but otherwise left the subordinates alone. It is generally accepted that learning plays a role in the establishment of most social dominance relationships (Rowell 1974; Wade 1978; Bernstein 1981; Flannelly and Blanchard 1981; Gauthreaux 1981). It is possible that subordinate *A. carolinensis* males have “learned” to behave in a particular manner (e.g. preemptively moving to lower perch sites) in order to reduce the chance of eliciting aggressive responses from dominant males.

The behavior of subordinate males changed from baseline isolate levels in every category that was tested (at least when dominant males were present in the same compartments). This is similar in nature to the theory put forth by Rowell (1974) that these relationships are driven by the subordinate males rather than the dominants. While it is correct to say that stable dominant-subordinate relationships depend on the submissiveness of subordinate animals, simply focusing on subordinates and “excluding” dominants only creates more problems. Ultimately, the relationships should probably not be called either dominance or subordination hierarchies but rather

“dominance-subordinance hierarchies” in recognition that the behaviors of *both* members have impacts on the nature of their relationship.

The fact that dominant animals show so few changes from their baseline levels while subordinates change in nearly every way is interesting, as it suggests that dominant behavior is reasonably close to “normal” behavior for these animals. This is similar to the conclusions of Brain (1981) mentioned earlier, who noted that the behavior of dominant mice was often comparable to the behavior of mice that were housed individually. The findings of this study were also consistent with others done in this lab (Greenberg et al. 1984; Greenberg and Crews 1990) that reported dominant behavior to be largely unchanged from isolate levels.

PATTERNS OF MOVEMENTS

The movement patterns of the paired animals were clearly not random ones. Subordinates not only avoided entering occupied compartments, but consistently moved out of occupied compartments as well. Given the chance to move away from the other animals they repeatedly did so. However, the relatively small size of the testing chamber meant that a subordinate could not actually escape the dominant male’s presence.

As for dominant males, although they did not actively avoid the subordinate, it is not entirely clear, simply by looking at the pattern of movements, whether or not they

were seeking out the subordinates. However, it was also observed that dominants and subordinates spent approximately 1/3 of their time together in the same compartment (Table 13). If the animals were moving through the testing chamber randomly, then this is the amount of time we would expect to see them together. Subordinates, though, were actively avoiding the dominant males, so the lizards should have been spending less time together than expected. Thus, the dominants appear to be actively seeking the subordinate males, causing the two animals to spend more time together than they otherwise would be.

Another piece of evidence to support this idea comes from the way in which subordinates moved through the testing chamber. Although dominant males spent relatively close to the same amount of time in each compartment, subordinates spent less than half as much time in the central compartment as they did in either of the end ones. The reason for this is not known, although it may have something to do with the fact that the central compartment has two doors instead of one. Subordinates may “prefer” end compartments because in those compartments they only have to watch one direction for a possible intruder. It could also be the case that subordinates move as far as possible when they change compartments and so they keep going until they are stopped in the end compartment. In any case, dominants did not show this bias against the center and divided their time more or less equally among the three compartments. Since the animals spent the “expected” amount of time together despite the fact that subordinates were avoiding an entire compartment, this serves as another

indication that at least one of the members of the pair is actively doing something to increase their time together

Future Studies

The data presented here suggest several areas for potential research. First, as has already been mentioned, a direct examination of the effects of hormone on patrolling rates (using castrates and implants) could help to determine how this behavior is controlled. A related issue would be to determine movement rates for isolate animals and then to perform hormone assays to determine what their relative levels of corticosterone and androgen actually are. A triangular cage setup could also provide some needed insight into the movement patterns of the animals. Using such a cage would eliminate the distinction between end compartments and center compartments, perhaps causing subordinate animals to move through the testing chamber more randomly than they currently do. It would also be helpful to use the current end to end setup but to selectively enrich one of the compartments to see if it had any impact on the movement patterns of either of the animals.

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