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LIFE WITH AND WITHOUT SEX: COMPARATIVE BEHAVIOR OF THREE SPECIES OF WHIPTAIL LIZARDS (CNEMIDOPHORUS: TEIIDAE)

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LIFE WITH AND WITHOUT SEX: COMPARATIVE BEHAVIOR OF THREE SPECIES OF WHIPTAIL LIZARDS (*CNEMIDOPHORUS*: TEIIDAE)

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BY

BETH EMILY LEUCK

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LIFE WITH AND WITHOUT SEX: COMPARATIVE BEHAVIOR OF THREE SPECIES OF WHIPTAIL LIZARDS (*CNEMIDOPHORUS*: TEIIDAE)

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PREFACE

This dissertation is prepared as two chapters. Each chapter will be submitted to a refereed journal. The first chapter will be submitted to Animal Behaviour, and the second chapter will be submitted to Copeia.

TABLE OF CONTENTS

Page

Chapter I

Chapter II

LIST OF TABLES

TABLE Page

Chapter I

Chapter II

LIST OF FIGURES

LIFE WITH AND WITHOUT SEX: COMPARATIVE SOCIAL BEHAVIOUR OF THREE SPECIES OF WHIPTAIL LIZARDS (*CNEMIDOPHORUS*: TEIIDAE)

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Abstract. Animals reproducing asexually, such as parthenogenetic animals, may share 100 percent of their genes with other population members. Because of this high genetic relatedness, kin selection may act on the behaviour of asexual animals. I studied two parthenogenetic and one bisexual species of whiptail lizards (Cnemidophorus) to find if parthenogens acted more nepotistically toward each other than bisexuals as predicted by kin selection theory. Aggressive interactions (supplanting, chasing and biting), competition over food items and fighting were less common in parthenogens than in bisexuals, indicating that the genetic relatedness of the parthenogens may affect behavioural differences. Organization of groups of five conspecific lizards into linear dominance hierarchies and the strength of these hierarchies were more dependent on the presence of males in the bisexual groups. Therefore, two factors potentially influencing differences in behaviour between parthenogenetic and bisexual whiptail lizards are the high degree of relatedness of the parthenogens and the absence of males in unisexual populations. Nepotistic behaviour was never observed among parthenogenetic whiptails for several possible reasons. First, it appears that members of parthenogenetic whiptail populations are not genetically identical due to independent origins of clones, mutation and/or recombination. Second, because parthenogenetic whiptail species are hybrids between two or three bisexual species, they may contain gene combinations that result in competitive rather than cooperative behaviour. Third, whiptail species do not defend resources, so opportunities for sharing or sacrificing resources are low.

Short title: LEUCK: SOCIAL BEHAVIOUR OF WHIPTAIL LIZARDS

(INTRODUCTION)

Asexually reproducing animals produce mitotically standardized offspring (Williams 1975) which are genetically identical, but sexually produced offspring share exactly one-half their genes with their parents and an average of one-half with their full sibs (Hamilton 1964a). The relatedness of an individual to other members of its species may be one factor affecting its behaviour toward them (Hamilton 1964a, 1964b). Because individuals are likely to maximize representation of their genes in succeeding generations (Williams 1966; Trivers 1972), an organism may cooperate with or aid another if the second individual is a close relative carrying a high percentage of the first individual's genes (Hamilton 1964a, 1964b). The fitness of the helper may be lowered but the fitness of the relative being helped may be raised; thus an individual may maximize its future gene representation through this nepotistic behaviour. The sum of an individual's own fitness plus the influence its nepotistic behaviour has on its close relatives' fitness is inclusive fitness (Hamilton 1964a, 1964b), and kin selection is selection for apparently altruistic activities among individuals sharing many genes. Asexual population members of identical genetic makeup, then, may exhibit a higher degree of nepotistic behaviour toward each other than bisexual animals.

One form of asexual reproduction is parthenogenesis, the development of egg cells not fertilized by male gametes (Uzzell 1970). Parthenogenetic females produce offspring genetically identical to themselves. For this reason parthenogenetic organisms possess identical genes if they are from one clone and may be less aggressive and more nepotistic toward each other than sexually reproducing organisms.

As well as being genetically identical, parthenogenetic populations differ from sexually reproducing populations by being all-female. The lack of males in parthenogenetic populations may contribute to lower levels of agonistic behaviour among members because males are often more aggressive than females (Williams 1966). Thus there are two factors, high genetic relatedness and absence of males, that may affect the behaviour of parthenogenetic animals and influence them to behave less aggressively and more nepotistically toward each other than bisexuals.

Among vertebrates all-female populations of fish, amphibians and reptiles are known to occur naturally (Uzzell 1970; White 1970). Although the ecology of unisexual vertebrate populations has been well studied (e.g. Moore & McKay 1971; Vrijenhoek 1978 for fishes; Uzzell 1964; Uzzell & Goldblatt 1967 for amphibians; Wright & Lowe 1968; Cuellar 1977, 1979; Schall 1976, 1977 for reptiles), little more than anecdotal observations have been reported on behaviour of unisexual vertebrates except for fish populations of the genus Poeciliopsis (McKay 1971). McKay did not address the effect of unisexuality on nepotistic or nonaggressive behaviour, so the hypotheses that genetic unity and lack of males in a population decrease agonistic behaviour have not yet been tested.

I investigated the effects of parthenogenesis and absence of males on the behaviour of whiptail lizards (genus Cnemidophorus). At least 13 species reproduce parthenogenetically (Cole 1975). Eight of them are found between the Rocky Mountains and Sierra Madre (Wright &

Lowe 1968) with the Rio Grande Valley of New Mexico as the center of distribution. Unisexual members of the genus were unknown until Maslin (1962) reported that he collected only females of six species and hypothesized that the lizards were reproducing without males. Several studies have confirmed that some members of the genus Cnemidophorus reproduce parthenogenetically (Cuellar 1968; Maslin 1971; Cole & Townsend 1977).

The 100 percent genetic relatedness of individuals in whiptail populations has been confirmed by histocompatibility studies (Maslin 1967; Cuellar 1976, 1977) and chromosome studies (Cole 1979). The relatedness is probably maintained through premeiotic endoduplication, but the mechanism has been studied in only one female of one parthenogenetic species (Cuellar 1971). Recently data from electrophoretic studies have cast doubts on the genetic unity of populations of one parthenogenetic species, C. tesselatus (Parker & Selander 1976; Parker 1979a), and this evidence will be discussed later.

While the probable genetic relatedness of individuals in populations of all-female whiptail lizards is 100 percent, the origin of these parthenogenetic "species" appears to be by hybridization of two bisexual species. Numerous studies have indicated that one complement of chromosomes is identical to the chromosomes of one bisexual species, and the other one or two complements (some whiptail parthenogens are triploid) are identical to the chromosomes of another bisexual species (Lowe & Wright 1966a, 1966b; Wright & Lowe 1967; Lowe et al. 1970; Bickham et al. 1976). Electrophoretic investigations (Neaves & Gerald 1968, 1969; Neaves 1969; McKinney et al. 1973), histocompatibility studies (Cuellar & McKinney 1976) and most recently examination of mitochondrial DNA (Brown & Wright 1979) have confirmed the hybrid origins of parthenogenetic Cnemidophorus populations.

Methods

Subjects

Because parthenogenetic whiptails are hybrid species, one chromosome complement will be identical to that of each parental bisexual species. These relationships allow behavioural comparisons of closely related species. To investigate the effects of parthenogenesis and lack of males on whiptail lizard behaviour, I chose to study Cnemidophorus tesselatus and C. neomexicanus (parthenogens) and the bisexual C. sexlineatus. Diploid C. tesselatus individuals are hybrids between two bisexual species, C. septemvittatus and C. tigris (Wright & Lowe 1964; Lowe et al. 1970; Parker & Selander 1976). In northeastern New Mexico and southeastern Colorado diploid C. tesselatus individuals apparently encountered bisexual C. sexlineatus populations and hybridised, producing triploid populations of C. tesselatus with chromosome complements from three different bisexual parents (Wright & Lowe 1967; Parker & Selander 1976). Cnemidophorus neomexicanus is a diploid parthenogen derived from bisexual C. inornatus and C. tigris (Lowe & Wright 1966a). Relationships of these whiptail complexes are diagrammed in Fig. 1.

I chose C. sexlineatus as the bisexual study species because more is known about it behaviourally than any other whiptail species. Investigations by Fitch (1958), Hardy (1962), Carpenter (1960, 1962) and Brackin (1976, 1978) have established basic behavioural patterns for the species. *Cnemidophorus tesselatus* was chosen because it was derived from and also hybridised with *C. sexlineatus*. Townsend (1979) and Cole (pers. comm.) suggested *C. neomexicanus* individuals are more aggressive toward each other than individuals of most bisexual species, so I studied *C. neomexicanus* to find if its behaviour contradicted the the predictions of kin selection theory. *C. tigris*, a parental species of both parthenogens, was not studied because of difficulties in capturing enough unharmed individuals for behavioural investigations.

Collection Sites

Diploid *C. tesselatus* and *C. sexlineatus* were collected at Conchas Lake State Park, San Miguel County, New Mexico. The site represents a potential hybridisation zone between the two species (Fig. 2). Triploid *C. tesselatus* individuals were collected at the Fremont County Sanitary Landfill, near Florence, Fremont County, Colorado; all known populations collected in the Arkansas River Valley of Colorado are triploid (Parker & Selander 1976). I confirmed the ploidy level of the Fremont County lizards by measuring RBC nuclei diameters and comparing them to RBC nuclei of *C. tesselatus* specimens from Conchas Lake which are known to be diploid (Wilbur 1976; Parker & Selander 1976). *Cnemidophorus neomexicanus* was collected along Tramway Boulevard in northeast Albuquerque, San Bernalillo County, New Mexico (Fig. 2).

Whiptails are fast, wary lizards which are difficult to capture uninjured. To avoid harming individuals, lizards were collected using a hardware cloth fence approximately 35 cm high and 4 m long (Cuellar 1971). Animals were herded into the fence by two to five persons and then caught by hand. No lizards were physically damaged, except for occasional tail losses, and many whiptails could be captured in a short time using this method.

Experimental Procedure

The collected whiptails were housed indoors at the Animal Behavior Laboratory, Department of Zoology, University of Oklahoma, Norman, in 38- to 189-litre terraria containing sandy substrates. Lizards were fed crickets and mealworms ad libitum, and cover, water and sunlight were provided to all terraria.

I used four 3 x 3 x 1-m outdoor galvanized metal enclosures for observations. The enclosures contained a sandy substrate that was cleared of most vegetation. In each enclosure two 39 x 19 x 19-cm concrete blocks, two rocks approximately 20 x 20 x 10 cm and a board approximately 60 x 30 cm offered cover; water was provided ad libitum. I observed the lizards from a 4-m high blind placed equidistant from the four pens so all pens could be seen at once. My presence did not seem to disturb the lizards.

I recorded behavioural data on 25 diploid _C_. _tesselatus_, 25 triploid _C_. _tesselatus_, 25 _C_. _neomexicanus_ and 75 _C_. _sexlineatus_ individuals. The three parthenogenetic groups were each divided into five replicates of five lizards. The bisexual lizards were divided into three groups of 25 lizards, and those groups were divided into five replicates of five lizards. The three _C_. _sexlineatus_ groups (five replicates in each) were: (1) all female lizards, (2) all male lizards and (3) mixed males and females (two replicates of three females and two males each and three replicates of two females and three males each).

I thus observed six groups of whiptails, three parthenogenetic and three bisexual, and each consisted of five five-lizard replicates.

Before initiating observations I marked individuals by enamel paint spots on their dorsa and bands of labeling tape around their tails. Even with the double marking system some lizards shed or rubbed off all marks within several days and had to be captured and remarked. I also recorded the sex and measured the snout-vent length of each lizard (Leuck 1980, Appendix B).

The five lizards of a replicate were placed in an enclosure and allowed to habituate for at least 24 hr. Then each replicate was observed for twenty 20-min periods. During the first seven observation periods cover (concrete blocks, rocks, board) was available for the lizards (Treatment 1). Approximately every other day after observations were terminated crickets were fed to the lizards. For the next seven periods (Treatment 2) two crickets per period were offered to create a potential food competition situation. During the remaining six periods (Treatment 3) all cover was removed, and crickets were offered only at the end of daily observations. Observations began on any one replicate in the four enclosures when more than two lizards were above ground. Then replicates were observed randomly according to which replicate contained the most number of lizards above ground. Daily observations terminated when lizards went under ground for the day. No replicate was observed for more than 140 min (seven periods) on any one day ($\bar{X}$ = 51 min; SD = 26 min; N = 234 days; a given day could be counted more than once because up to four replicates might be observed on that day), and observations on each replicate were completed in six to 11 days. The lizards were observed June to September 1977-1979, usually from 8.30 to 14.30 hours, Central Standard Time, when whiptails are most active (Leuck MS).

I recorded the following data on checksheets during each 20-min observation period: (1) aggressive interactions-- recorded by which lizard supplanted (displaced another lizard in space), chased or bit which other lizard, (2) co-resting-- if two or more lizards rested within 15 cm of each other, (3) which lizards captured crickets offered during Treatment 2 (cricket periods), (4) activity-- recorded for each lizard above ground as basking or resting in shade; foraging in sun or shade and (5) following of one lizard by another. The aggressive interaction data were used to determine dominance relationships. A portable cassette tape recorder was used to record observations not listed on the checksheet, such as prolonged fighting, lack of aggression during cricket periods or cloacal rubbing (Leuck unpubl. data).

Analysis

Analysis of variance, Student-Newman-Keuls test, chi-square goodness of fit test, Pearson product-moment correlation coefficient and Wilcoxon two-sample test were used to analyse results (Sokal and Rohlf 1969). Raw data on which statistical tests were performed are listed in Appendices A to G of Leuck (1980). Because all five lizards of a replicate were not above ground during each observation period, I derived a variable called "lizard-periods" to standardize comparisons of data among six groups. A lizard-period is one lizard above ground for one 20-min observation period. During observation periods the above-ground number of lizards in a replicate varied from two to five. If the number of lizards above ground in each period is summed for all 20 observation periods, values can range from 40 (two lizards per period x 20 periods) to 100 (five lizards per period x 20 periods). This value was calculated for each replicate. Actual lizard-period values ranged from 52 for two diploid C. tesselatus replicates to 92 for a C. neomexicanus replicate with a mean of 77 lizard-periods per replicate (SD = 11.2; N = 30 replicates). Dividing the number of aggressive interactions and co-resting of each replicate by lizard-periods provided standardized values for the number of above-ground lizards.

I recorded aggressive interactions between all pairs of above-ground lizards in a replicate. When all aggressive interactions (supplanting, chasing and biting) which lizard A won against lizard B were compared to the interactions B won against A, one lizard usually emerged dominant and one subordinate. In some pairs the dominant won almost all the interactions, but in other pairs the subordinate won nearly as many interactions as the dominant. To assess variation in the number of interactions won by two lizards of a pair I derived a dominance strength index (DSI) for each replicate. Five lizards per replicate yield 10 possible dyadic interactions. The number of encounters won by the dominant lizard of a dyad is divided into encounters won by the subordinant, and the 10 dyadic interactions of lizards in a replicate are summed to derive a DSI for each replicate as follows:

$$\text{DSI} = \sum_{n=1}^{10} \left(\frac{\text{interactions won by subordinate} + 1}{\text{interactions won by dominant} + 1} \right)$$

One is added to the numerator and denominator to avoid zeroes. If the dominant of each dyad in a replicate wins most encounters with the subordinate, the DSI approaches zero. If the two lizards of every dyad in a replicate win an equal number of encounters the DSI is 10. Therefore lower values indicate stronger dominance relations among the lizards of a replicate.

Results

Aggressive Interactions

Parthenogenetic individuals were less aggressive toward each other than were bisexuals (Table I). Supplanting was the most common aggressive interaction in all groups, and biting the least common. Male C. sexlineatus replicates had the highest rates of supplanting but individuals in mixed-sex C. sexlineatus replicates chased and bit more than lizards in other groups. Rates of all aggressive encounters were higher in bisexual than in parthenogenetic groups, but chasing and biting rates in bisexual groups were not significantly different from each other.

The percentage of total aggressive interactions of each type is shown in Fig. 3. A higher percentage of total interactions was attributable to supplanting, a "mild" aggressive act, in parthenogenetic groups than in bisexual groups. Triploid C. tesselatus individuals rarely chased and bit (less than 0.4 percent), but in mixed-sex replicates 32 percent of all interactions were chasing and biting (more "violent" acts than supplanting). Nineteen percent of the interactions in diploid C. tesselatus, 10 percent in C. neomexicanus, 24 percent in female C. sexlineatus and 26 percent in male C. sexlineatus replicates were chasing and biting.

The rates of supplanting, chasing and biting did not vary significantly among treatments with two exceptions. During Treatment 2 (crickets offered as food), diploid C. tesselatus replicates chased more and C. neomexicanus replicates bit more. Removing structure from the enclosure (Treatment 3) did not affect aggressive interactions in any group.

Treatment 2 introduced potential competition among the five lizards of a replicate. When a lizard captured a cricket, it could eat the cricket: (1) out of sight of other lizards, (2) near other lizards and be ignored by them or (3) near other lizards and be chased by one of them. Occasionally a lizard would run under a board or rock after capturing a cricket, but usually the cricket was consumed where captured.

Parthenogens were more likely to consume crickets near each other without chasing or being chased than were bisexuals (Wilcoxon two-sample test; $U = 9.0$; $P < 0.05$; Fig. 4). However, a bisexual whiptail with a cricket was chased or chased significantly more often than a parthenogen with a cricket (Wilcoxon two-sample test; $U = 9.0$; $P < 0.05$; Fig. 4). I observed feeding frenzies during cricket periods in two diploid C. tesselatus replicates and one C. neomexicanus replicate. During feeding frenzies all lizards above ground chased each other when one or two of the five lizards were carrying crickets. These frenzies may have occurred in parthenogenetic rather than in bisexual replicates because the dominance relationships (discussed later) were weaker among the parthenogens, and one or two lizards did not dominate the movement of all other lizards in the enclosure. The feeding frenzies undoubtedly contributed to the significantly higher rates of chasing in diploid C. tesselatus replicates and biting in C. neomexicanus replicates observed during Treatment 2.

The most violent social interactions were tumbling, biting fights (tumble fights) which lasted up to several seconds. No parthenogens were observed to tumble fight, but all bisexual groups did (Fig. 5). The interaction did not seem to be a component of courtship because more male than male-female pairs tumble fought, and copulation was not seen to follow tumble fighting between males and females. However, tumble fighting was more common between males in the mixed-sex C. sexlineatus than in the all-male group. The difference may be due to competition among males in the mixed-sex group to inseminate females (Williams 1966). Because no females were present in the all-male replicates, no insemination competition was possible.

Dominance Relationships

Differences in group dominance relationships, determined by DSI values, were due to the presence or absence of males (Table II). The four groups containing all females had significantly higher DSI values than did groups containing males, indicating weaker dominance relationships in each female replicate. In addition, four out of five and five out of five replicates were organized into linear dominance hierarchies in the mixed-sex and male C. sexlineatus groups respectively. None of the C. tesselatus replicates and only one replicate each of the C. neomexicanus and female C. sexlineatus groups were organized into linear dominance hierarchies. In the mixed-sex C. sexlineatus replicates males dominated more lizards than did females (Wilcoxon two-sample test; $U = 132.0$; $P < 0.05$; Fig. 6).

Hierarchy position has been correlated with body length and ability to obtain food in C. sexlineatus. Carpenter (1960) and Hardy

(1962) found no correlation of snout-vent length with hierarchy position, but Brackin (1978) found high-ranking individuals were longer than low-ranking lizards. In all groups except the diploid C. tesselatus group longer lizards were the more dominant individuals (Fig. 7). Hardy (1962) stated that dominants obtained food more readily than subordinates, but Brackin (1978) found no such correlation. I found that dominant individuals of the triploid C. tesselatus and C. neomexicanus groups obtained significantly more crickets than subordinates during Treatment 2, but no relationship between rank and food was apparent in the other groups (X^2 test; expected values generated by dividing the number of lizards of 25 in each rank category [0-4] by 25 [five lizards x five replicates] and multiplying 70 crickets [seven periods x two crickets x five replicates] by this value).

Tolerance and Non-aggressive Interactions

Parthenogenetic whiptails rested near each other (closer than 15 cm) more often than did bisexual whiptails (Table III). Two males rested within 15 cm of each other only once, but in parthenogenetic groups co-resting was more frequent (up to 105 times in the C. neomexicanus group). In the mixed-sex C. sexlineatus group females rested near females five times and next to males six times, but males rested next to males only once.

Whiptail lizards sometimes follow each other while foraging. If parthenogens cooperate to find food, then following should occur more often than in bisexuals. I found no significant differences in following among the six groups. The highest occurrence of following (22) was in the mixed-sex C. sexlineatus group and may have been related to courtship because males followed females 17 times. Females followed males twice, females followed females once and males followed males twice. These values differed significantly from four expected (average) values of 5.5 ($X^2 = 32.18$; $P<0.05$).

Discussion

I predicted two factors of parthenogenetic whiptail lizard population structure might influence differences in behaviour between parthenogenetic and bisexual groups. First, the high degree of relatedness among parthenogens was hypothesized to increase the amount of nepotistic behaviour observed, and second, the absence of males was hypothesized to decrease the amount of aggression over that observed in bisexual lizards.

The most obvious difference between unisexual and bisexual groups was in aggression levels. All three parthenogenetic groups had lower supplanting, chasing and biting rates than bisexuals, but bisexual groups containing males had higher rates than the bisexual group composed of females. Therefore, both factors, relatedness and male absence, might have contributed to differences in aggression. The same trend (parthenogens with lowest rates- female bisexuals intermediate- groups with males highest) was apparent among other behavioural attributes measured.

According to kin selection theory unisexual whiptail lizards should be less aggressive toward each other than bisexuals. If parthenogens are genetically identical, being aggressive toward a conspecific would be similar to being aggressive toward one's self. However, I never observed a total lack of agonistic behaviour among parthenogens. If no aggression had been observed, it would appear that the genetic relatedness of the individuals strongly influenced social interactions and absence of males was probably not an important factor. Aggression was not absent but levels differed among unisexual and bisexual groups. Whether genetic similarity or absence of males was more important in determining a particular behavioural attribute thus became a problem best solved by statistical analysis. If the degree of relatedness of the parthenogens was the influencing factor, then the three parthenogenetic groups would be more similar to each other in behaviour than they would be to the bisexual groups. If the lack of males influenced differences of a particular behavioural attribute, then the all-female *C. sexlineatus* group would more closely resemble the parthenogens than it would conspecific groups containing males.

The genetic relatedness of the parthenogens seemed to affect differences in aggression rates of all types among groups (Table IV). Either the three parthenogenetic groups differed significantly from the three bisexual groups (chasing and biting), or the combined data for the unisexual groups differed significantly from the combined bisexual group data (tumble fighting, chases involving a lizard with a cricket or eating near other lizards without interaction). A high percentage of aggressive acts consisted of supplanting (a "mild" aggressive interaction) in parthenogenetic groups, but in bisexual groups more interactions were attributable to chasing and biting ("violent" aggressive acts) than in unisexual groups. When parthenogens engaged in aggressive acts, they were more likely to engage in less violent interactions than were *C. sexlineatus* individuals. Variations in co-resting, a benign interaction, also seemed to be affected by the relatedness of the parthenogens because co-resting means of the bisexual groups did not differ significantly.

In contrast, the all-female *C. sexlineatus* group more closely resembled the unisexual groups in formation and maintenance of dominance hierarchies. The presence of males seemed to influence the maintenance of a strict social order such as a linear dominance hierarchy. Although *C. sexlineatus* females were almost as aggressive as males, higher-ranking individuals did not always win aggressive encounters with lower-ranking individuals. If dominant *C. sexlineatus* males always won over subordinate males, then DSI values for the five replicates would have approached zero. Instead values averaged 3.3, which implies males also did not have a perfect hierarchy in which dominants always won. Brackin (1978) reported that dominant *C. sexlineatus* males were never chased or bitten by subordinates but this was not the case in my study.

If parthenogenetic whiptails are 100 percent related to each other, why did they not behave nepotistically toward each other? In fact, they not only were non-nepotists, but also occasionally fought. Part of the problem may lie with the assumption that populations of unisexual whiptails are genetically identical. When Parker and Selander (1976) examined diploid populations of *C. tesselatus* electrophoretically, they found that individuals varied at six of 21 loci studied, indicating the existence of 12 possible clones. In combination with morphological variation previously studied by Zweifel (1965), possibly 17 distinct clones of diploid *C. tesselatus* populations exist (Parker 1979a). Parker and Selander (1976) and Parker (1979a, 1979b) proposed that the existing diploid *C. tesselatus* clones may have arisen by multiple hybridisation events, mutation or recombination. At Conchas Lake, where diploid *C. tesselatus* individuals were collected for my study, up to seven clones may inhabit areas around the reservoir, and these clones may have had multiple origins (Parker 1979a). Parker (1979b) suggested that *C. tigris* and *C. septemvittatus*, which hybridised to produce the diploid *C. tesselatus* form, had once inhabited northeastern New Mexico. They hybridised many times in the region, then for unknown reasons receded southward to where they are now sympatric in the Texas Big Bend region, leaving clones of *C. tesselatus* in northeastern New Mexico (Parker 1979b).

Triploid *C. tesselatus* populations may represent only one clone because Parker and Selander (1976) and Parker (1979a) found no genotypic variation in triploid populations studied. The population I used in this study was not examined by Parker and Selander, but phenotypically it conforms to Zweifel's (1965) Pattern Class B description. Other Pattern Class B populations examined by Parker and Selander (1976) composed one clone. Therefore the triploid individuals I used are likely to be from a single clone.

If diploid *C. tesselatus* individuals vary genetically and triploid individuals do not, then diploid lizards may be more aggressive than triploids because their confidence of genetic relatedness is lower. Rates of supplanting are higher in triploid *C. tesselatus* replicates (Table I), but rates of "violent" aggressive interactions, chasing and biting, are higher in diploid replicates. A higher percentage of total aggressive interactions is attributable to chasing and biting in the diploid replicates (Fig. 3). Two feeding frenzies were observed in diploid replicates but none in triploid replicates (Fig. 4), and triploid checkered whiptails co-rested over twice as many times as diploid lizards (Table III). However, the average DSI value for the diploid *C. tesselatus* group was higher than the triploid *C. tesselatus* group value indicating weaker dominance relationships among the lizards less related to each other. Also puzzling was the fact that the diploid group was the only one not to show a significant correlation of size with hierarchy position.

Generally, more closely related lizards were less aggressive toward and more tolerant of each other, but cooperation as predicted by kin selection theory was never observed. Even if individuals of a population share all their genes, these genes are derived from two to three separate chromosome sets of ancestral bisexual species. These chromosomes come from individuals normally in competition for resources and carrying no gene combinations promoting nepotism, and there may not have been enough time for the resulting parthenogenetic species to accumulate mutations affecting nepotistic behaviour. Parthenogenetic whiptails may be 12 000 years old (Axtell 1966) or they may have developed as late as 200 B.P. when domestic cattle destroyed southwestern United States grasslands creating disturbed "weedy" habitats where bisexual species may have come in contact and the resulting hybrid parthenogens thrived (Wright & Lowe 1968; Lowe et al. 1970; Parker & Selander 1976). These possible recent origins of parthenogenetic whiptails might account for their lack of nepotistic behaviour and the presence of low aggression levels even in triploid *C. tesselatus* individuals 100 percent related to each other.

However, kin selection theory may still apply to the behaviour of parthenogenetic whiptail lizards. Aggression, though present, occurred at significantly lower levels than in bisexual whiptails. The strongest evidence supporting the operation of kin selection on parthenogenetic populations comes from the total lack of tumble fighting in all three unisexual groups. Therefore, although nepotism was not observed, neither was escalated fighting which was commonly seen in bisexual whiptails. There seems to be evidence that parthenogenetic whiptails treat conspecifics as if they were close relatives.

Opportunities for parthenogens to act nepotistically may be limited due to the lack of sociality in whiptail lizards. No parental care of eggs and young occur in any known whiptails, so parthenogens probably do not share duties with relatives in raising young. Food donating or sharing would be one possible nepotistic act, but this phenomenon was never recorded. Perhaps allowing a conspecific to eat a food item (cricket) without attempting to steal it is a nepotistic act, particularly on the part of a dominant individual which would otherwise secure all food items for itself. Crews and Fitzgerald (1980) may have observed nepotism in parthenogenetic *C. uniparens*, *C. velox* and *C. tesselatus* individuals. Females not reproductively active (no yolking follicles) mounted and pseudocopulated with conspecifics with large preovulatory follicles. Crews and Fitzgerald (1980) propose this behaviour may be necessary to prime the reproductively active lizard for egg-laying. If this hypothesis is correct, then the lizard acting like a male may benefit from its masculine behaviour because the egg-laying female passes genes shared by both lizards on to her offspring. However, I did not observe such "lesbian" behaviour in my study.

An animal cannot be a nepotist if it does not defend a resource which it may relinquish to another in an act of nepotism. North American whiptail lizards do not maintain territories (Fitch 1958; Carpenter 1960; Hardy 1962; Stamps 1977), and I did not observe them defending food resources, burrows, basking sites or eggs and young. Because Cnemidophorus species are active foragers they do not defend stationary food sources, and burrows seem relatively easy to dig, so they may not be defended either (Stamps 1977). Not only, then, does the lack of defense reduce the opportunity for nepotistic behaviour, but it also reduces the possible sources of aggression in a whiptail lizard population.

However, males seem to defend females, and males' aggressiveness toward each other may be due to each one defending a female or females to assure himself a copulation to pass on his genes. Male aggressiveness may be genetically mediated (Williams 1966), so aggression levels are high even in all-male groups of whiptails.

I observed copulation in the mixed-sex C. sexlineatus replicates four times. In one case the second ranking male began copulating but was dragged off the female by the highest ranking male, who then copulated with the same female. On another occasion the highest ranking male found and copulated with a female just seconds after the second ranking male had mated with her. Thus male aggressiveness may be related to attempts to control a defensible limited resource and may also involve sperm competition to assure fertilization by one's own gametes over those of a competitor. Because copulation is not a normal component of the parthenogens' social organization, one opportunity for the existence of nepotism by sharing or sacrificing mates is missing.

In conclusion, kin selection may influence some aspects of the behaviour of parthenogenetic *Cnemidophorus* species, although it may not be possible to separate the effects of genetic relatedness from the absence of males in parthenogenetic populations. Aggressive interactions, particularly escalated fighting, were significantly less common in unisexuals than bisexuals, but hierarchy relationships depended on the presence of males. My observations suggest that kin selection may be operating on these lizards to reduce aggressiveness so mature members of a parthenogenetic population have an opportunity to transmit genes shared with all other members of their population to succeeding generations.

Acknowledgments

This paper constituted a portion of my doctoral dissertation at the University of Oklahoma. Many people generously helped collect lizards for this study, but I particularly thank Edwin Leuck and Ross Sherwood not only for their constant help in the field but also for many thoughtful discussions on whiptail behaviour and ecology. John Wright also discussed problems of *Cnemidophorus* parthenogenesis with me, and I am indebted to him for his knowledgeable opinions on the subject. Gary Schnell, Alan Covich and especially Bedford Vestal made helpful comments on the manuscript, and I am grateful to Charles Carpenter for his encouragement and advice during the study. A Sigma Xi Grant-in-Aid of Research provided financial support for portions of the research.

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Table I. Mean Occurrences per Lizard-period (See Text) of Supplanting, Chasing and Biting in Six Groups of Whiptail Lizards*

Supplanting

DIP TES	TRIP TES	NEO	F SEX	MIX SEX	M SEX
0.73	1.00	1.23	1.25	1.44	2.24
(0.42-1.03)	(0.83-1.16)	(0.91-1.54)	(0.86-1.63)	(0.41-2.47)	(0.92-3.56)

Chasing

TRIP TES	NEO	DIP TES	F SEX	M SEX	MIX SEX
0.03	0.08	0.16	0.25	0.51	0.51
(-0.01-0.08)	(0.00-0.15)	(0.01-0.31)	(0.16-0.34)	(0.30-0.71)	(0.05-0.96)

Biting

TRIP TES	DIP TES	NEO	F SEX	M SEX	MIX SEX
0.01	0.04	0.06	0.15	0.16	0.25
(-0.01-0.03)	(-0.02-0.11)	(0.03-0.10)	(0.07-0.24)	(0.05-0.21)	(0.03-0.48)

*Ninety-five percent confidence limits for each mean are given in parentheses. Means not connected by a common underline are significantly different at $P < 0.05$. DIP TES = diploid *C. tesselatus*, TRIP TES = triploid *C. tesselatus*, NEO = *C. neomexicanus*, F SEX = all-female *C. sexlineatus*, MIX SEX = mixed male and female *C. sexlineatus*, M SEX = all-male *C. sexlineatus*. N = five replicates per mean.

Table II. Mean Dominance Strength Indices (See Text) for Six Groups of Whiptail Lizards*

M SEX	MIX SEX	F SEX	NEO	TRIP TES	DIP TES
3.29	3.72	5.40	5.52	5.90	6.28
(2.29-4.28)	(2.21-5.23)	(3.93-6.87)	(1.48-2.47)	(5.13-6.76)	(5.08-7.48)

*Ninety-five percent confidence limits for each mean are given in parentheses. Means not connected by a common underline are significantly different at $P<0.05$. N = five replicates per mean. Abbreviations are the same as in Table I.

Table III. Mean Number of Times per Lizard-period (See Text) that Whiptail Lizards of Six Groups Rested Closer Than 15 cm to Each Other*

M SEX	MIX SEX	F SEX	DIP TES	TRIP TES	NEO
0.002	0.03	0.05	0.09	0.15	0.26
(0.00-0.01)	(0.00-0.06)	(0.00-0.09)	(0.07-0.12)	(0.09-0.21)	(0.18-0.33)
1**	12	20	27	58	105

*Ninety-five percent confidence limits for each mean are given in parentheses. Means not connected by a common underline are significantly different at $P<0.05$. N = five replicates per mean.

**Total occurrences of co-resting recorded for each group. Abbreviations are the same as in Table I.

Table IV. Apparent Effects of High Genetic Relatedness of Parthenogenetic Whiptail Lizards or Absence of Males in Whiptail Lizard Groups as Factors Affecting Behavioural Differences among Groups*

	Influencing factor:		
	Genetic Similarity	Absence of Males	Uncertain
Supplanting rates	*		
Chasing and biting rates	*		
Tumble fighting	*		
Eating without interaction	*		
Percent each aggressive category contributes to total interactions			*
Co-resting	*		
Dominance Strength Index		*	
Linear dominance hierarchy		*	
Body length correlated with status			*

*If the three parthenogenetic groups closely resemble each other statistically, then genetic relatedness may be the influencing factor. If the four groups containing all females (three parthenogenetic + one bisexual) closely resemble each other, then the absence of males may be the influencing factor.

FIGURE LEGENDS

Fig. 1. Relationships of some hybrid all-female *Cnemidophorus* species to their bisexual parental species. Names of species used in this study are shown in boxes.

Fig. 2. Ranges (partial for *C. sexlineatus*) and collection sites for three *Cnemidophorus* species used in this study. *C. neomexicanus* was collected at Albuquerque, New Mexico, *C. tesselatus* (diploid) and *C. sexlineatus* were collected at Conchas Lake, New Mexico, and *C. tesselatus* (triploid) was collected near Florence, Colorado.

Fig. 3. Supplanting, chasing and biting as percentages of total aggressive interactions for six groups of whiptail lizards. TRIP TES = triploid *C. tesselatus*, NEO = *C. neomexicanus*, DIP TES = diploid *C. tesselatus*, F SEX = all-female *C. sexlineatus*, M SEX = all-male *C. sexlineatus*, MIX SEX = mixed male and female *C. sexlineatus*. Parthenogenetic groups are shown in boxes.

Fig. 4. Number of times whiptail lizards (1) ate crickets near others without an ensuing interaction (above the horizontal line) and (2) chased a lizard carrying a cricket (below the horizontal line). Abbreviations are the same as in Fig. 3. Parthenogenetic groups are shown in boxes.

Fig. 5. Number of tumble fights (escalated fighting) observed in six groups of whiptail lizards. Abbreviations are the same as in Fig. 3. Parthenogenetic groups are shown in boxes.

Fig. 6. Number of females and males dominating zero through four other lizards in the mixed-sex *C. sexlineatus* group. Males dominated significantly more lizards than did females (Wilcoxon two-sample test; $U = 132.0$; $P < 0.05$).

Fig. 7. Relation of snout-vent length to number of lizards dominated in *Cnemidophorus* groups (r = product-moment correlation coefficient). Abbreviations are the same as in Fig. 3. Parthenogenetic groups are shown in boxes.

Figure 1

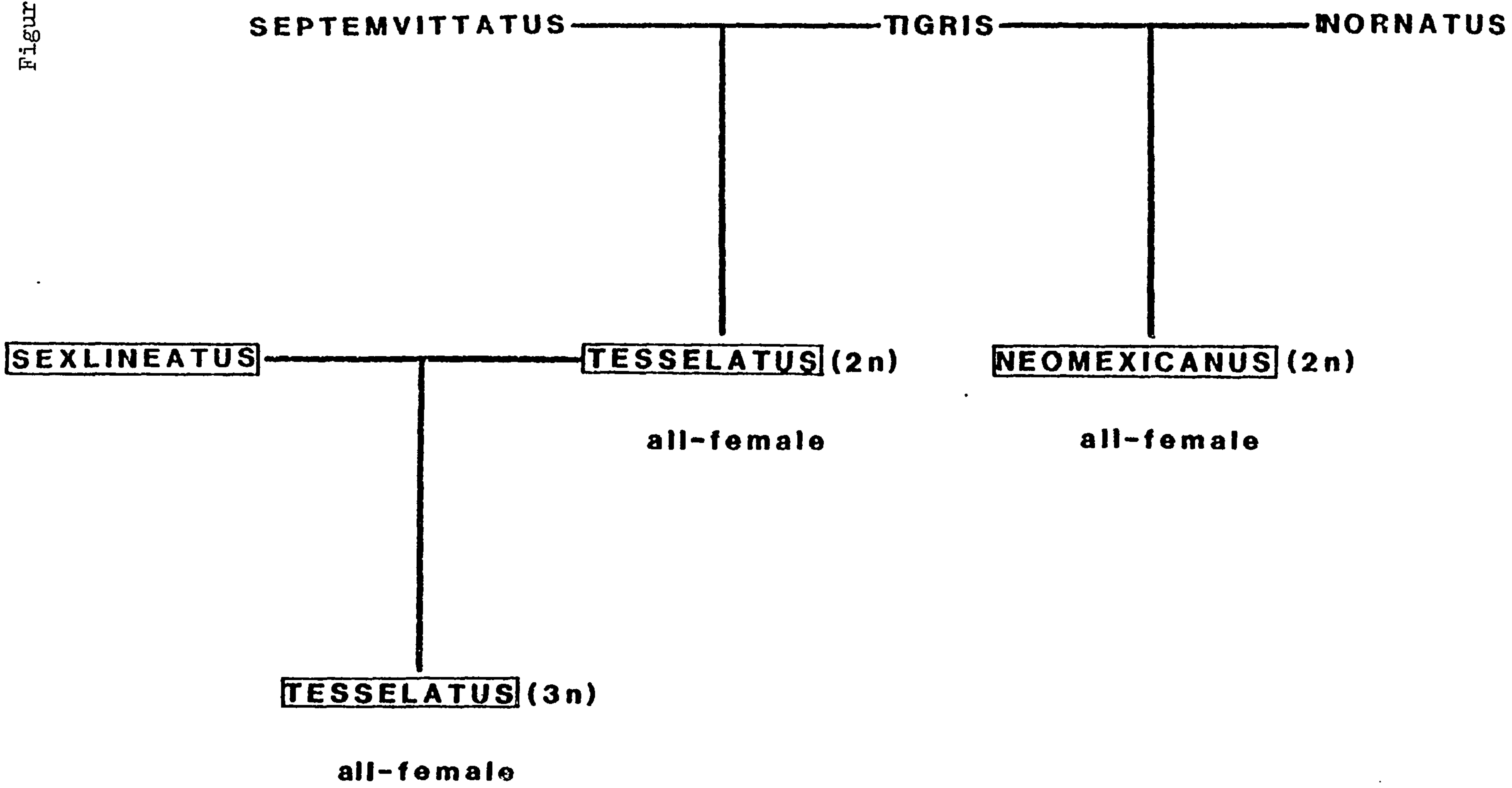

SEPTEMVITTATUS
TIGRIS
INORNATUS
SEXLINEATUS
TESSELATUS (2n)
all-female
NEOMEXICANUS (2n)
all-female
TESSELATUS (3n)
all-female

Figure 2

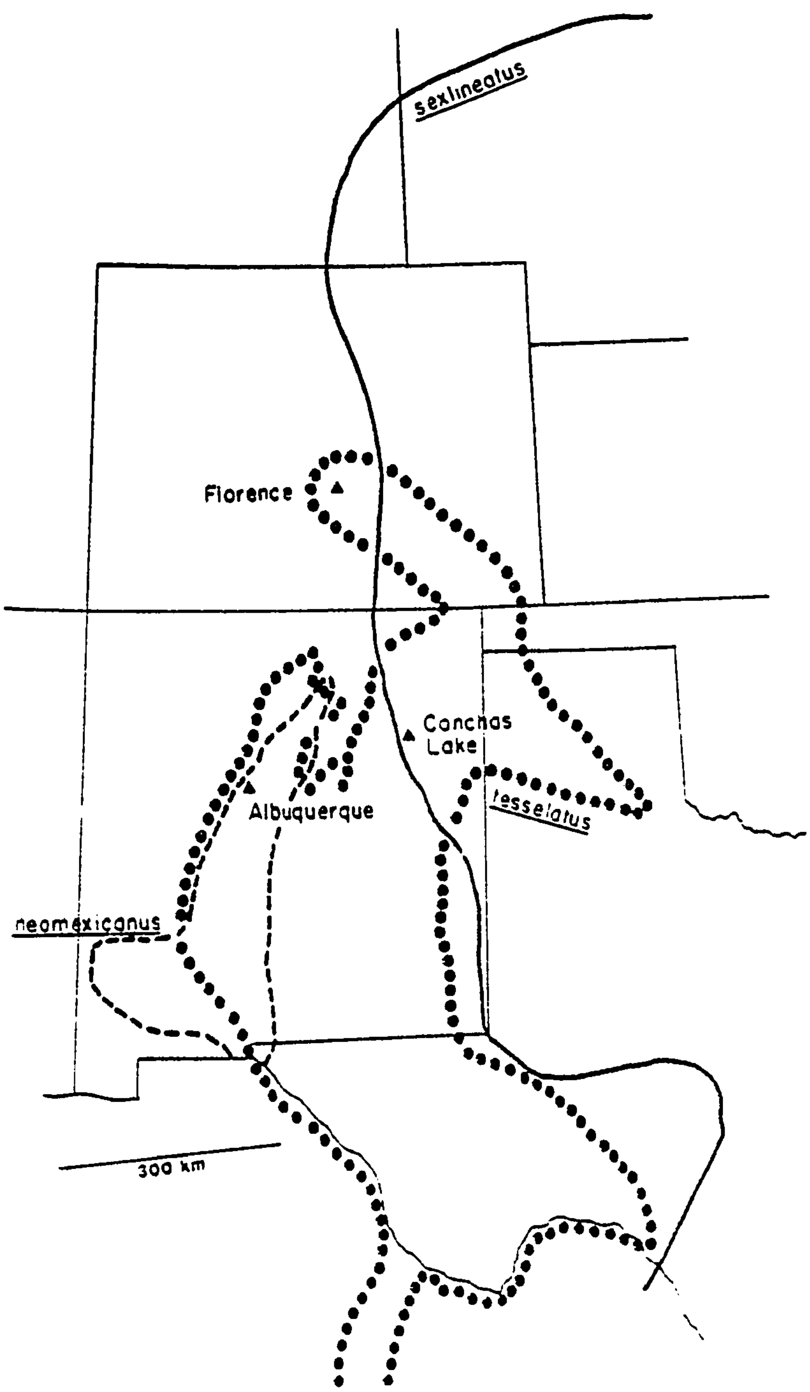

sexlineatus
Florence
Conchas Lake
tesselatus
Albuquerque
neomexicanus
300 km

Figure 3

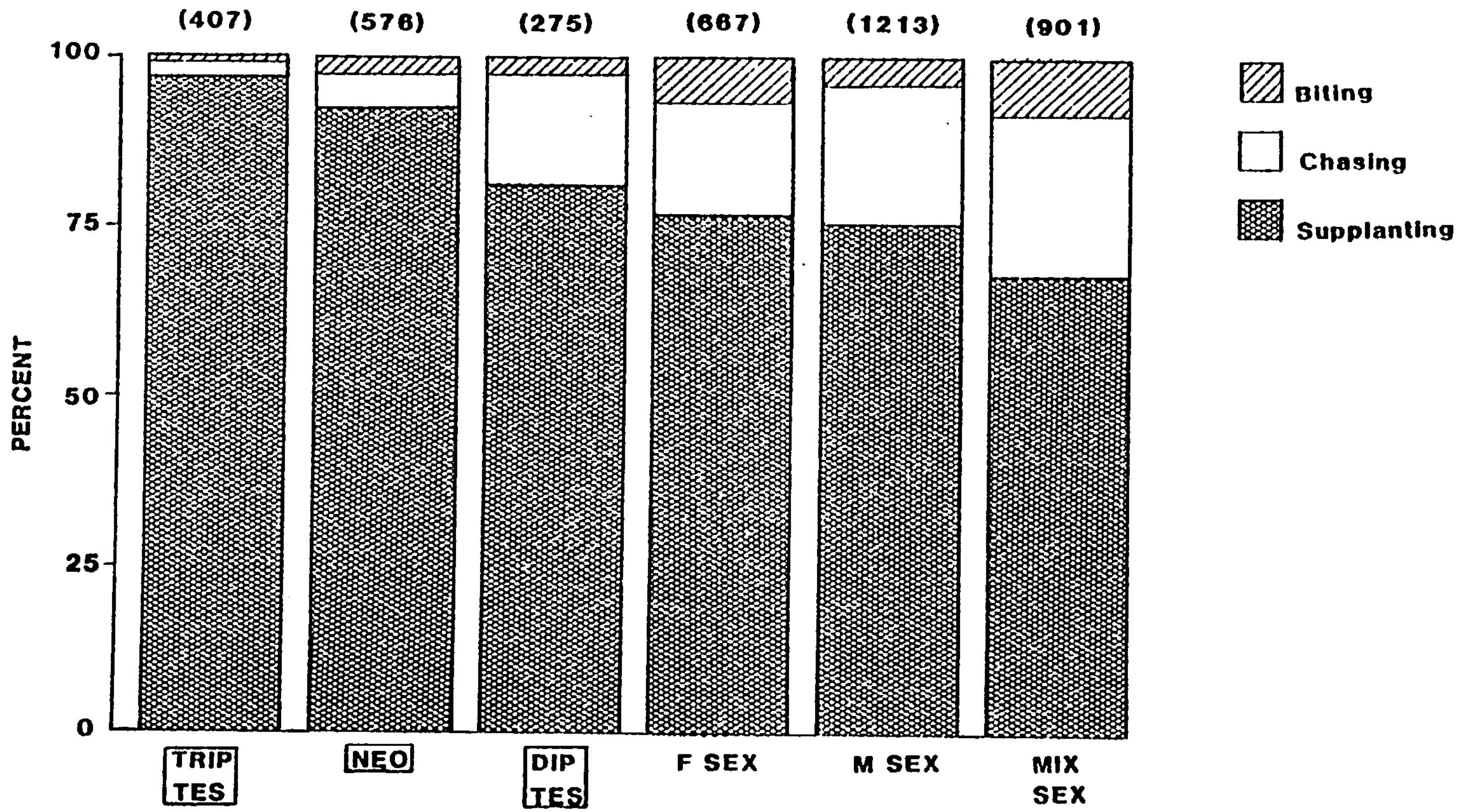

(407)
(576)
(275)
(667)
(1213)
(901)
100
75
50
25
0
PERCENT
TRIP TES
NEO
DIP TES
F SEX
M SEX
MIX SEX
▨ Biting
☐ Chasing
▩ Supplanting

Figure 4

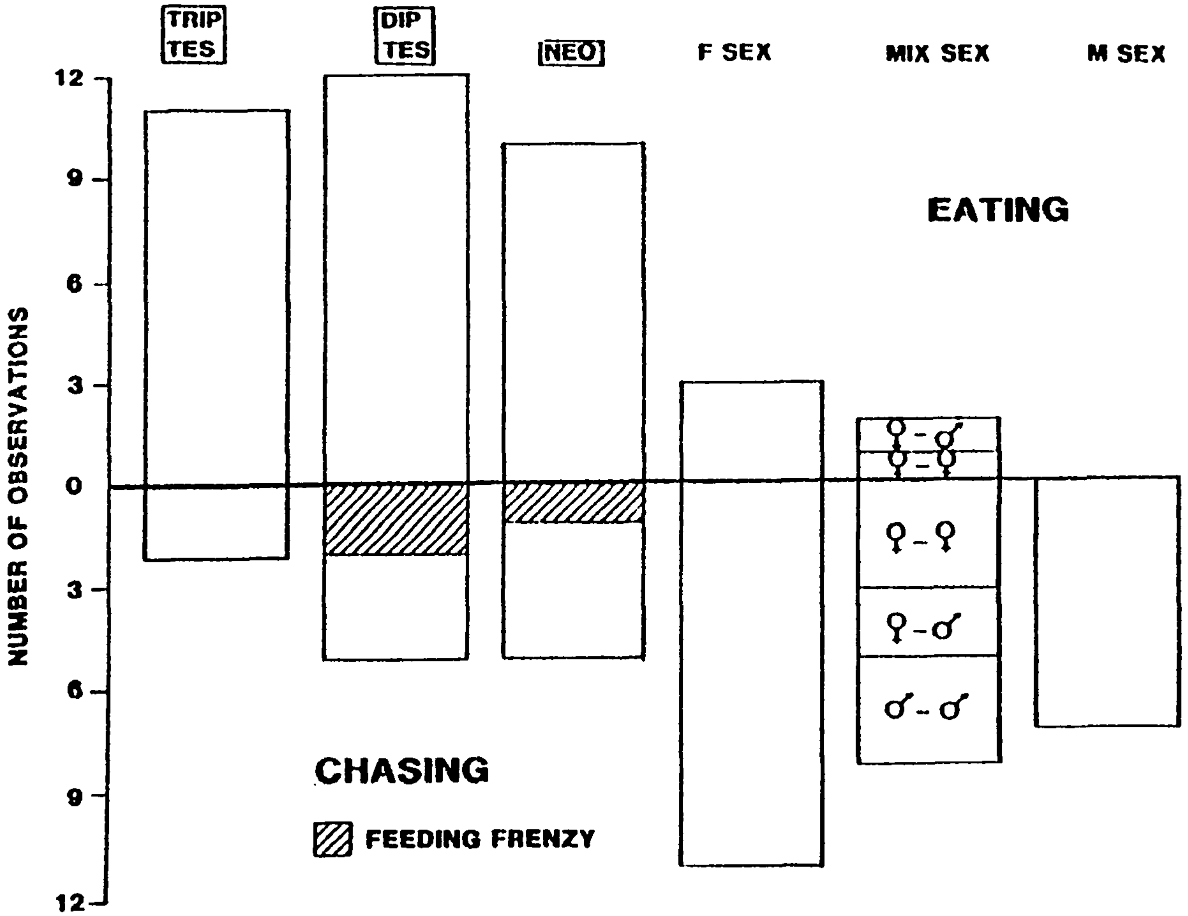

TRIP TES
DIP TES
NEO
F SEX
MIX SEX
M SEX
12
9
6
3
0
3
6
9
12
NUMBER OF OBSERVATIONS
EATING
CHASING
▨ FEEDING FRENZY
♀-♂
♀-♀
♀-♀
♀-♂
♂-♂

Figure 5

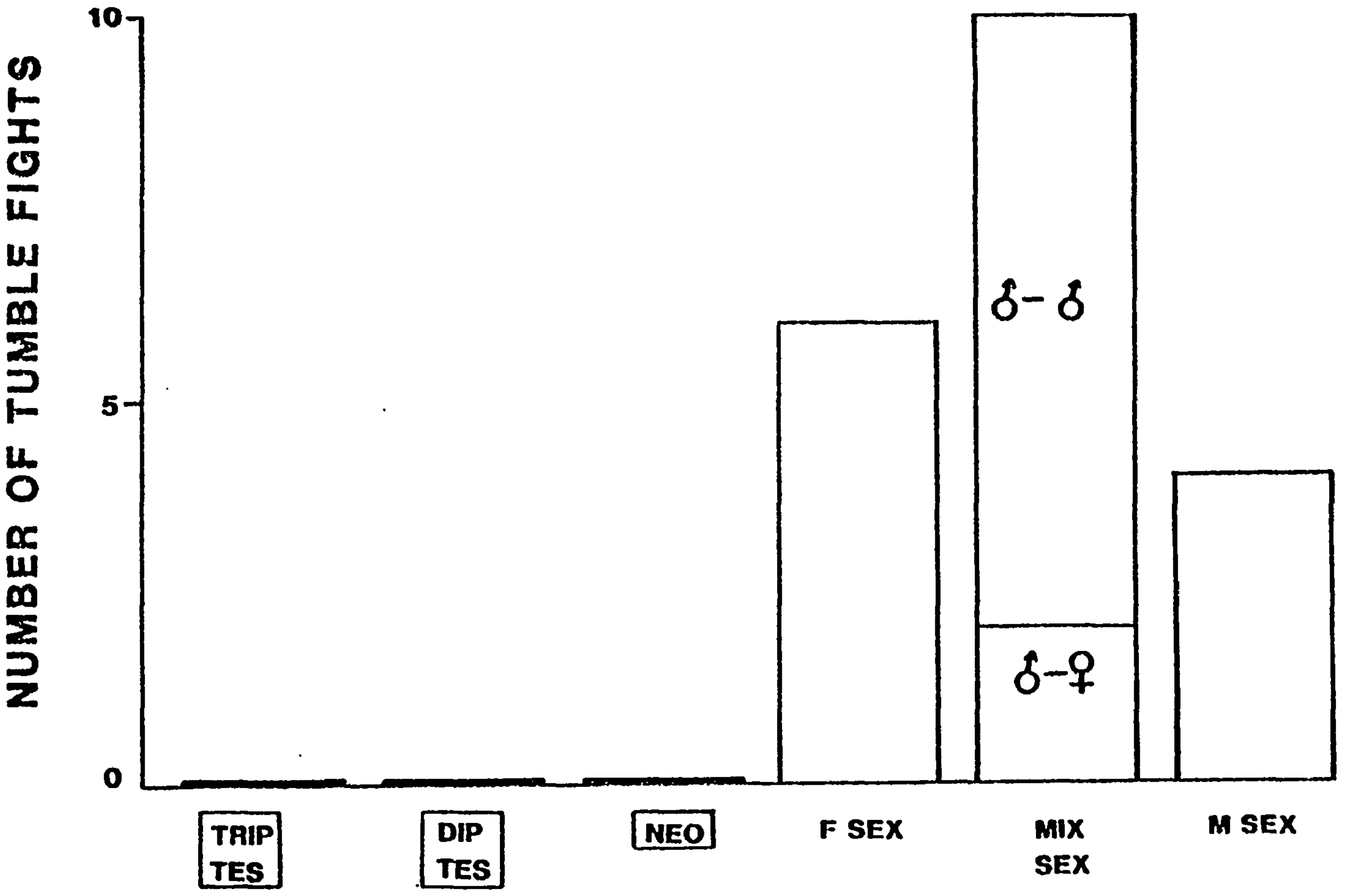

NUMBER OF TUMBLE FIGHTS
10
5
0
TRIP TES
DIP TES
NEO
F SEX
MIX SEX
M SEX
♂–♂
♂–♀

Figure 6

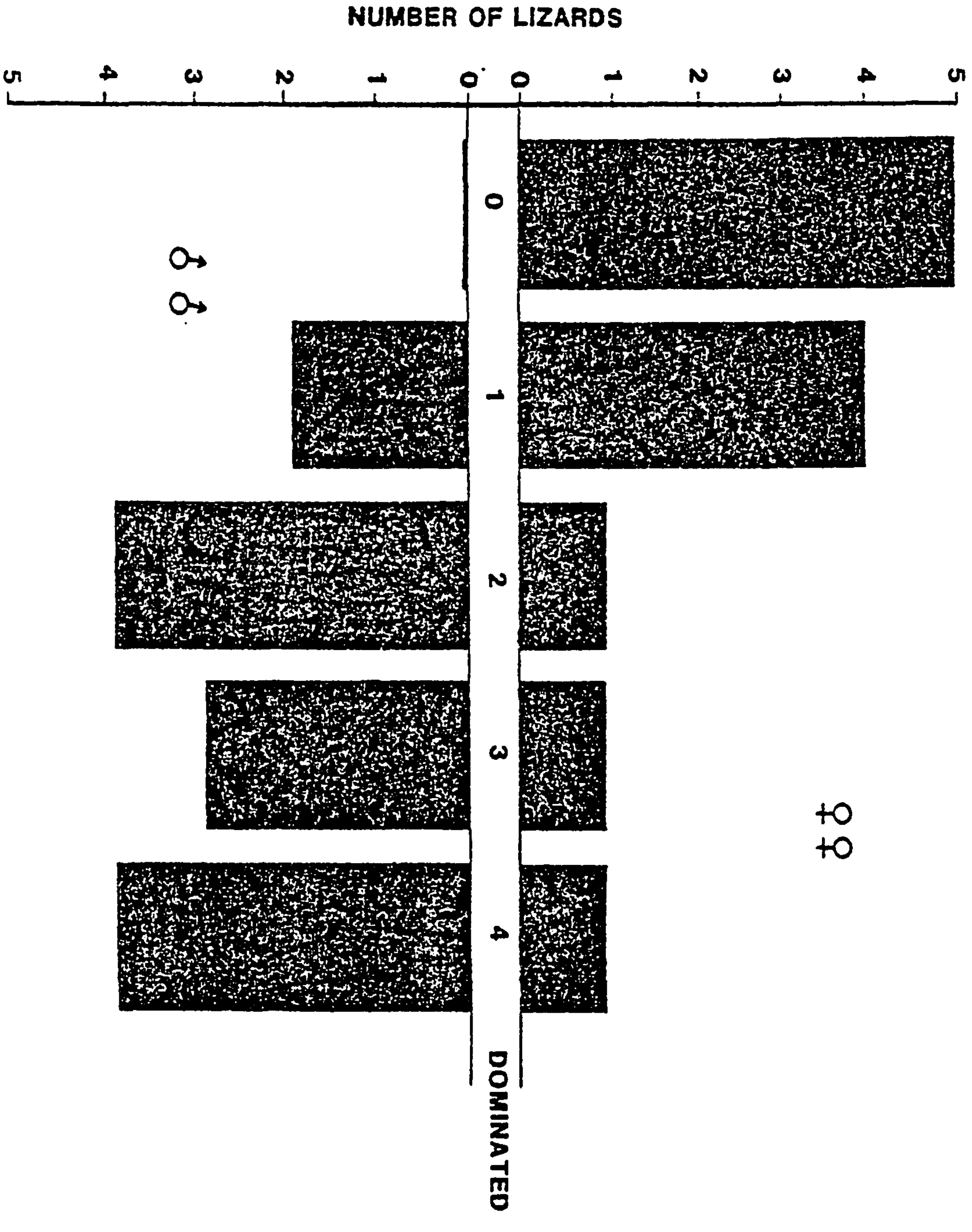
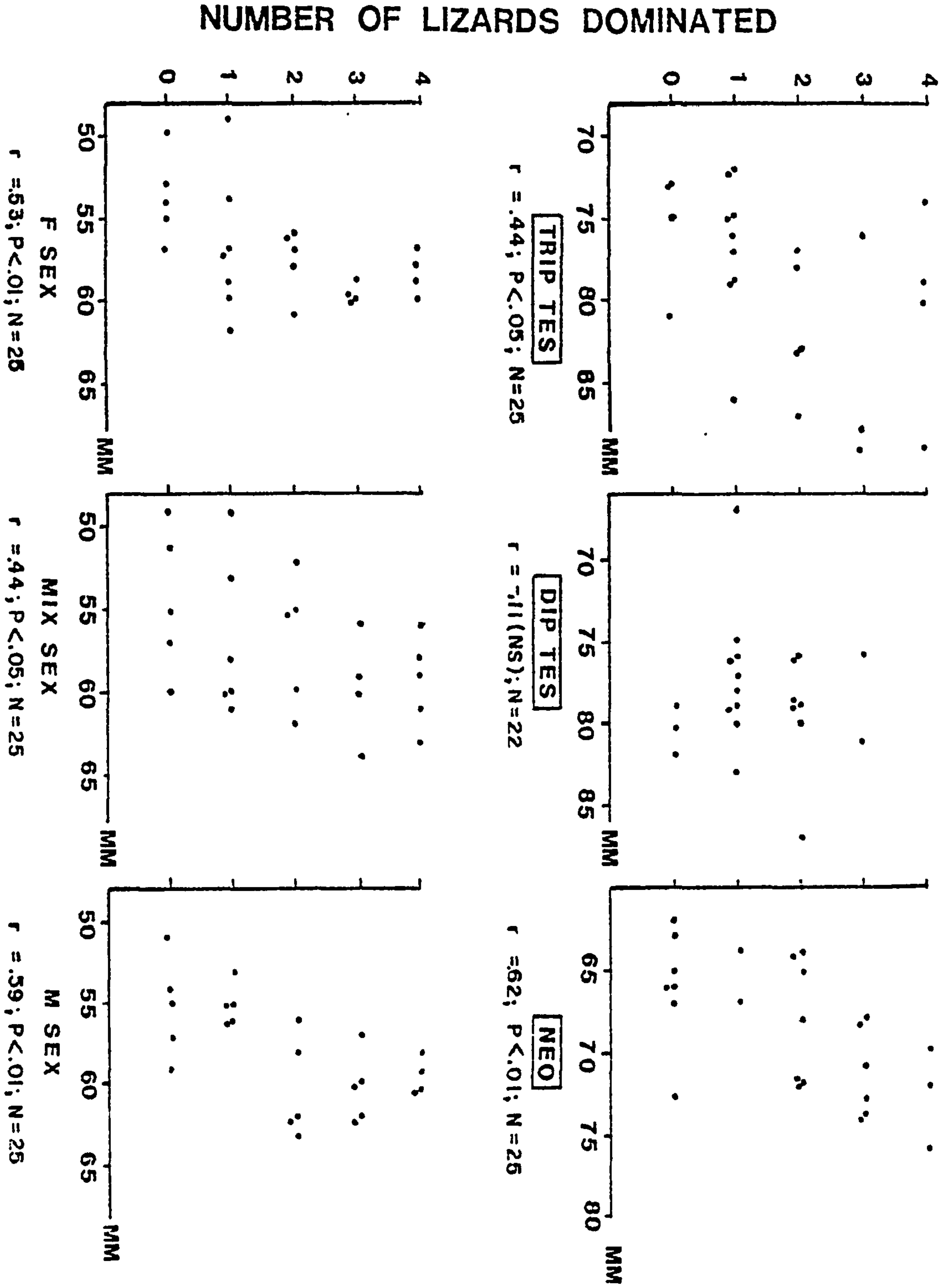


Figure 7


NUMBER OF LIZARDS DOMINATED
0
1
2
3
4
MM
TRIP TES
r = .44; P<.05; N=25
DIP TES
r = -.11 (NS); N=22
NEO
r =.62; P<.01; N=25
F SEX
r =.53; P<.01; N=25
MIX SEX
r =.44; P<.05; N=25
M SEX
r =.59; P<.01; N=25
70
75
80
85
65
50
55
60

COMPARATIVE BURROW USE AND ACTIVITY PATTERNS OF PARTHENOGENETIC AND BISEXUAL WHIPTAIL LIZARDS (*CNEMIDOPHORUS*: TEIIDAE)

Beth E. Leuck

(ABSTRACT)

Some whiptail lizards (*Cnemidophorus*) reproduce parthenogenetically; thus conspecific parthenogens may be genetically identical. This high degree of relatedness may lead to cooperative space use by parthenogenetic lizards, while bisexual whiptails, which are less related to each other, may compete for limited spatial features. I studied groups of five conspecific lizards of *Cnemidophorus tesselatus* and *C. neomexicanus* (parthenogenetic) and *C. sexlineatus* (bisexual) in identical outdoor enclosures to find if space use and activity differed. Parthenogens used a significantly greater number of sites for digging burrows than did the more site-specific bisexuals. Neither type of whiptail maintained territories nor defended objects to the exclusion of conspecifics, and both shared objects under which they burrowed (burrow sites). Parthenogens shared actual burrows (nine occurrences), but only one case of burrow sharing among bisexuals was observed. As the number of lizards above ground in each enclosure increased, aggression levels increased significantly in *C. sexlineatus* groups containing males, indicating males may control the aggressive characteristics of a group. Activity above ground in all whiptail lizard groups peaked in late morning to early afternoon, but no trends correlating activity with daily high temperatures were apparent. Therefore, space use and activity may have been affected by three factors: (1) differences in genetic relatedness of parthenogens and bisexuals, (2) presence or absence of

males in groups and (3) species-specific differences. Separating the effects of these parameters on space use and activity is difficult.

(INTRODUCTION)

Animals usually are not randomly distributed in space but orient with respect to animate and inanimate objects in their environment (Brown and Orians, 1970; Wilson, 1972). Inanimate spatial features of potential significance are topographical and vegetational variations in the habitat (Wilson, 1972); animate features include other animals with which living space is shared. Both types of features can result in attraction or repulsion of individuals and ultimately determine the distribution of a population in space (Brown and Orians, 1970).

Many parameters of space use by individuals, such as whether an animal maintains a territory or lives colonially or solitarily in a particular habitat, may be determined by selective forces acting over time (Davies, 1978). The morphology of an individual and its perception of environmental features (King, 1970) may affect how it reacts to animate and inanimate features and utilizes space.

The relatedness of an organism to conspecifics may affect its spatial response to animate factors, particularly to other population members. Animals that share a large number of genes (i.e. are close relatives) may show a high degree of tolerance for and cooperation with relatives because doing so increases the inclusive fitness of the related individuals (Hamilton, 1964a, 1964b). The spatial organization of closely related individuals may be different from the organization of less related conspecifics which are in competition with each other to increase their genetic contribution (Williams, 1966). Closely related organisms, then, should share limited inanimate features in the environment if sharing increases the fitness of related individuals.

Less related organisms should attempt to control limited inanimate features for their own use and exclude conspecifics.

Comparing space use of phylogenetically closely related species whose members share different percentages of genes with conspecifics may help determine to what extent genes affect spatial patterns, particularly if inanimate factors are held constant. In this study I investigate the relation of genetic similarity to space use and activity patterns in parthenogenetic and bisexual whiptail lizards (Cnemidophorus). Although several authors have investigated habitat use of whiptail lizards (e.g. Medica, 1967; Wright and Lowe, 1968; Schall, 1976; Cuellar, 1979), no study of Cnemidophorus species has held environmental factors constant to assess the effects of genetic differences on the spatial behavior of parthenogentic and bisexual whiptails.

Parthenogenesis, a form of asexual reproduction in which eggs are not fertilized by male gametes (Uzzell, 1970), results in all-female offspring identical to the reproducing female (clones). Some North American whiptail lizards reproduce in this manner, resulting in populations in which individuals may share 100% of their genes (Cuellar, 1968; Maslin, 1971; Cole, 1975; Cole and Townsend, 1977). Because members of parthenogenetic whiptail lizard populations are genetically very similar or identical, they may cooperatively utilize limited inanimate spatial features, such as burrowing and basking sites, while less related bisexual whiptails may compete for the same features.

The origin of all-female whiptail lizards is by hybridization of two bisexual whiptail species. Numerous studies have indicated that one complement of chromosomes is identical to the chromosomes of one bisexual species, and the other one or two complements (some whiptail parthenogens are triploid) are identical to the chromosomes of another bisexual species (Lowe and Wright, 1966a, 1966b; Wright and Lowe, 1967; Lowe et al., 1970; Bickham et al., 1976). Electrophoretic investigations (Neaves and Gerald, 1968, 1969; Neaves, 1969; McKinney et al., 1973), histocompatibility studies (Cuellar and McKinney, 1976) and most recently examination of mitochondrial DNA (Brown and Wright, 1979) have confirmed the hybrid origins of parthenogenetic *Cnemidophorus* populations.

Methods

Because parthenogenetic whiptails are hybrid species, one chromosome complement will be identical to that of each parental bisexual species. These relationships allow behavioral comparisons of closely related species. To investigate the effect of genetic relatedness on space use by whiptails I studied *Cnemidophorus tesselatus* and *C. neomexicanus* (parthenogenetic) and *C. sexlineatus* (bisexual). Currently the taxonomic designation *C. tesselatus* refers to both diploid and triploid populations; the triploid populations are derived from hybridization of diploid *C. tesselatus* individuals with male *C. sexlineatus* individuals (Wright and Lowe, 1967; Parker and Selander, 1976). *Cnemidophorus neomexicanus* is a diploid parthenogen derived from the bisexual species *C. tigris* and *C. inornatus* (Lowe and Wright, 1966a). Relationships of these parthenogenetic lizards to their parental species are shown in Fig. 1.

Collection methods and sites are described in Leuck (MS). *Cnemidophorus neomexicanus* was collected in Albuquerque, New Mexico, diploid *C. tesselatus* and *C. sexlineatus* at Conchas Lake State Park, New

Mexico, and triploid C. tesselatus near Florence, Colorado. After collection lizards were brought to the Animal Behavior Laboratory, Department of Zoology, University of Oklahoma, Norman, and housed in 38- 189-litre (10- 50-gallon) terraria containing sandy substrates. Lizards were fed crickets and mealworms ad libitum, and cover, water and sunlight were provided to all terraria.

I used four outdoor galvanized metal enclosures, 3 m x 3 m x 1 m, for observations. The enclosures contained a sandy substrate that was cleared of most vegetation. In each enclosure two concrete blocks (39 cm x 19 cm x 19 cm), two rocks approximately 20 cm x 20 cm x 10 cm and a board approximately 60 cm x 30 cm offered cover, and water was provided ad libitum (Fig. 2). I observed the lizards from a 4 m high blind placed equidistant from the four pens so all pens could be seen at once. My presence did not seem to disturb the lizards.

I recorded behavioral data on 25 diploid C. tesselatus, 25 triploid C. tesselatus, 25 C. neomexicanus and 75 C. sexlineatus individuals. The three parthenogenetic groups were divided into five replicates of five lizards. The bisexual group was divided into three groups of 25 lizards, and those groups were subdivided into five replicates of five lizards. The three C. sexlineatus groups (five replicates in each) were composed as follows: (1) all female lizards, (2) all male lizards and (3) mixed males and females (two replicates of three females and two males each and three replicates of two females and three males each). In total I observed six groups of whiptails, three parthenogenetic, three bisexual, and each group consisted of five five-lizard replicates.

Before initiating observations I marked individuals by painting spots on their dorsa with enamel paint and wrapping different numbers of bands of labeling tape around their tails. Even with the double marking system several lizards shed or rubbed off all marks within several days and had to be captured and remarked. I also recorded the sex and measured the snout-vent of each lizard (Leuck, 1980, Appendix B).

Five lizards of a replicate were placed in an enclosure and allowed to habituate for at least 24 h. Then the lizards of each replicate were observed for twenty 20-min periods. During the first 14 periods the structures described previously were present in the enclosure; however, for the final six periods objects were removed to evaluate whether or not space use by the lizards was altered. No replicate was observed for more than 140 min (seven periods) on any day ($\bar{X} = 51$ min; SD = 26 min; N = 234 days; a given day could be counted more than once because up to four replicates might be observed on that day), and observations on each replicate were completed in six to 11 days. After a replicate was removed and before another was placed in an enclosure, the substrate was hoed to destroy any burrows constructed by the five previous occupants. Lizards were observed June to September 1977-1979, usually from 0830 to 1430, Central Standard Time, when whiptails are most active (Leuck, 1980, Appendix F).

I recorded the following data to determine space use and activity patterns during each 20-min period: (1) place of emergence if lizard emerged from a burrow during the period; (2) place of retreat if lizard retreated to a burrow and remained there for 5 min or until observations on that replicate were terminated; (3) activity, which was recorded for each lizard above ground as basking, resting in shade, or foraging in sun or shade; and (4) aggressive interactions, which were recorded by which lizard supplanted (displaced another lizard in space) chased or bit which other lizard. I also recorded the high temperature for each date on which observations were made (obtained from the National Severe Storms Laboratory, Department of Commerce, Max Westheimer Airfield, Norman, OK, approximately 1 km from the Animal Behavior Laboratory) (Leuck, 1980, Appendix G).

Chi square goodness of fit tests, tests of independence and Pearson product-moment correlation coefficients were used in analyses (Sokal and Rohlf, 1969). Raw data on which statistical tests were performed are listed in Leuck (1980). To assess the association of aggression (supplanting + chasing + biting) with temperature it was necessary to account for the number of lizards above ground during each period. During observations the above-ground number of lizards in a replicate varied from two to five lizards (observations were begun only when at least two lizards were above ground). To determine aggression rates in each replicate observed on a given day, I summed the number of above-ground lizards in a replicate during each period on that date (one lizard above ground for one period = one lizard-period) and divided the total number of aggressive interactions observed for that replicate by the number of lizard-periods. For example, if one replicate was observed for three 20-min periods on a given day; four lizards were above ground during each period; 7, 5 and 11 aggressive interactions were recorded for the three periods, then the rate of aggression for that replicate for that date would be (7 + 5 + 11 interactions)/(4 lizards x

3 periods) = 1.92 interactions per lizard-period. These standardized rates were used to compare number of aggressive interactions when two, three, four or five lizards were above ground. Aggression rates at different temperatures were also compared.

I recorded aggressive interactions between all possible pairs of lizards in a replicate (five lizards per replicate yield 10 dyads). When all aggressive interactions (supplanting + chasing + biting) which lizard A won against lizard B were compared to interactions B won against A, one of the two was usually dominant. Dominance relationships were calculated for each dyad in each replicate. The lizards of each replicate were then assigned ranks depending on the number of other lizards they dominated. A lizard dominating four lizards of a replicate was ranked 4, while a lizard dominating no other lizards ranked 0. I then compared structure use and activity among lizards in different rank categories.

Results and Discussion

Use of structure in the enclosure.-- Lizards could dig burrows under six objects in an enclosure (Fig. 2), along the walls or in the open sand. Object use by lizards of five of the six groups differed from average expected use; only all-female C. sexlineatus individuals seemed to burrow equally under all the objects in the enclosures (Table 1). Two of three parthenogenetic groups (the two C. tesselatus groups) frequently constructed burrows in open sand, but open areas were not used as often by C. neomexicanus and bisexual groups. The most heavily utilized object for burrowing by all groups was the board. Parthenogenetic lizards used burrows significantly more often than bisexuals (comparison of expected [average] values from Table 1 for parthenogens to expected values for bisexuals; single classification analysis of variance; $F = 58.03$; $P<0.01$).

All groups shifted burrowing areas when objects were removed from the enclosures after fourteen 20-min periods (Table 2). With objects in the enclosures, both parthenogens and bisexuals burrowed under them frequently. After removal burrowing shifted from the sand where objects had been located to open sand and along walls of the enclosures. In the triploid *C. tesselatus*, *C. neomexicanus*, mixed-sex *C. sexlineatus* and all-male *C. sexlineatus* groups more lizards constructed burrows along walls after object removal than in any other location. Most diploid *C. tesselatus* individuals burrowed in open sand, and *C. sexlineatus* females used both the sand over which objects had been placed and the sand along walls after object removal.

Parthenogenetic lizards used significantly more sites for burrows than did bisexual whiptails (Table 3). Fifty-nine percent of all unisexual whiptails observed burrowing used three to six sites for burrows, but only 4% of all bisexual whiptails used more than two sites. The lack of site specificity seen in unisexual whiptails may be related not only to their genetic similarity to conspecifics, but also to their possible propensity for disturbed habitats (Wright and Lowe, 1968; Cuellar, 1977) where environmental fluctuations are constantly destroying burrows. In the more stable habitats that Wright and Lowe (1968) suggest bisexual whiptails inhabit, site specificity can be maintained because burrows are not continually disturbed. The use of open sand for burrows varied among the species I studied; more *C. tesselatus* individuals burrowed in open sand than other whiptails. Schall (1976) found *C. tesselatus* in open areas 33.8% of the time that he sighted individuals. Cuellar (1977) stated that rocky canyons are often considered prime habitat for the species, but he believed all North American parthenogenetic whiptails inhabit continually flooded riverine habitats where burrows are regularly destroyed. The habitat of *C. neomexicanus* has not yet been examined, but in my study its burrowing under objects rather than in open sand seemed to more closely resemble the behavior of bisexuals. However, like the *C. tesselatus* groups it showed less site specificity than the bisexual *C. sexlineatus* groups.

No whiptail lizard was observed defending an object under which it had burrowed; objects over burrows were shared with conspecifics in all groups. In only one case did bisexual lizards actually share burrows (a male and a female in a mixed-sex *C. sexlineatus* replicate), but parthenogens were found sharing burrows nine times (four cases in the triploid *C. tesselatus*, four in the diploid *C. tesselatus* and one in the *C. neomexicanus* group).

Burrow sharing is a type of cooperative space use pattern predicted to occur in parthenogenetic whiptails. However, the sharing of burrows was probably not a sign of cooperation but an indication of tolerance. Differences in co-resting and dominance strength indices between parthenogens and bisexuals (Leuck, MS) also indicated that parthenogenetic whiptails are tolerant of each other but probably do not cooperate. In addition, tolerance of conspecifics in burrows may extend to the two *C. tesselatus* groups because only one occurrence of burrow sharing was observed in *C. neomexicanus*. When I maintained the latter species in indoor terraria, individuals spread out and hid under different objects. In contrast, C. tesselatus individuals were often found hiding together under one object, even if two or three were available. Thus, C. neomexicanus may closely resemble bisexuals in unshared burrow use, and its behavioral deviation from other parthenogenetic groups is difficult to explain.

Parthenogenetic and bisexual whiptail lizards did not defend burrow sites, and there seemed to be no control of particular objects by high-ranking lizards of either reproductive type. If one object was preferred for burrowing (such as the board), it might be expected that more high-ranking than low-ranking individuals would be found under that object. However, when object use by lizards in each rank category was compared to expected use (based on the number of lizards in each rank category for each group), no significant differences were apparent in any of the groups. Lack of territoriality and/or object ownership is probably a general social characteristic of many Cnemidophorus species (Fitch, 1958; Carpenter, 1960; Hardy, 1962; Stamps, 1977).

Activity and aggression.-- Whiptail lizards are heliophilic animals that are most active in late morning and early afternoon. No differences in activity patterns between unisexual and bisexual groups were evident in this study (Fig. 3), but in all groups more lizards were above ground from 0930- 1230 than during any other time of day.

Whiptail lizards have been reported to have a bimodal activity pattern in the field (Milstead, 1957a, 1957b; Carpenter, 1961; Echternacht, 1967; Medica, 1967; Schall, 1976). The peak activity period is usually late morning to early afternoon, but a second lesser activity peak occurs in the late afternoon. Although I periodically checked all replicates for late afternoon activity, I rarely observed lizards above ground after 1530. This phenomenon may have been an artifact of captivity, but it may also have related to the geographic areas from which lizards were collected. The field studies in which a late afternoon activity period has been reported were carried out in Oklahoma (Carpenter, 1961), Texas (Milstead, 1957a, 1957b; Schall, 1976), southern New Mexico (Medica, 1967) or southern Arizona (Echternacht, 1967). I collected lizards in northern New Mexico and Colorado where daily high temperatures were lower than in Oklahoma, Texas, southern New Mexico and Arizona (United States Department of Agriculture, 1941). *Cnemidophorus* species in cooler climates may not have a second daily activity period. Barden (1942) maintained *C. sexlineatus* individuals from Indiana and Kansas under various light-dark and temperature regimes in the laboratory and found only one late morning activity peak. While collecting whiptails in New Mexico and Colorado I did not observe late afternoon activity in the field. The lack of a late afternoon activity period in northern *Cnemidophorus* populations may be due to selective forces acting on the populations because I did not record afternoon activity in the collected lizards in Norman, Oklahoma, even though Norman's average July temperature is higher than July averages recorded in northern New Mexico and Colorado (United States Department of Agriculture, 1941).

No differences between unisexuals and bisexuals in length of activity periods or time of peak activity were apparent in this study. Schall (1976) found variations in time of activity among five species of whiptail lizards, but differences did not follow a parthenogenetic-bisexual dichotomy. Asplund (1974) attributed activity differences to size differences in the *Cnemidophorus* species he studied, and slight variations I observed may also be due to size differences among *C. tesselatus*, *C. neomexicanus* and *C. sexlineatus*. Sex differences may also exist in *C. sexlineatus*. The mixed-sex group reached peak activity at 0930, the all-female group at 1030 and the all-male group at 1130.

Aggressive interactions per lizard-period increased as more lizards were above ground in every group (Fig. 4). The correlation of number of lizards above ground with aggressive interactions per lizard-period was significant in three groups, including the two bisexual groups containing males. *Cnemidophorus sexlineatus* males were more aggressive than females of any of the species studied (Leuck, MS), and males' intolerance of conspecifics contributed to an increase in aggression as the number of males in a limited space increased. In addition, high-ranking males were particularly belligerent toward other males. The rates of individual aggression among high-ranking males in the all-male and mixed-sex *C. sexlineatus* replicates were considerably higher than rates of aggression recorded for high-ranking females in parthenogenetic and all-female bisexual groups. A higher degree of aggressiveness among males than females is common to many species (Williams, 1966).

Although general whiptail lizard activity (basking, foraging, etc.) has been correlated with ambient temperature in the field (Carpenter, 1961; Asplund, 1974; Schall, 1976, 1977), observations on the relationship of social behavior and temperature have not yet been reported. I found no trends correlating aggressive interactions and temperature in my study. In only two replicates of 30 (one triplo

C. tesselatus and one all-female C. sexlineatus) did aggression rates significantly increase with an increase in temperature. No other positive or negative correlations were found in other replicates, so it seems that ambient temperature does not affect rates of social interactions among whiptail lizards.

Conclusions.-- I predicted that parthenogenetic whiptails would cooperate and share limited inanimate spatial features while bisexuals would compete with enclosure mates for the same resources. Other differences, such as variations in time of activity and habitat use, were also expected. The only factors which seemed associated with genetic differences between unisexuals and bisexuals were burrow site specificity and burrow sharing. Parthenogens used more areas for constructing burrows than did bisexuals and as predicted shared burrows while bisexuals did not. No true cooperation like that seen in some other extremely closely related organisms (Hamilton, 1964b) was observed among unisexual whiptails, but their tolerance of conspecifics was higher than bisexuals' tolerance for each other.

Other variables measured did not show significant differences between parthenogens and bisexuals. Time of activity and defense of resources did not differ between the two types of whiptails. Variation in one other trait seemed to depend on the presence or absence of males in the replicates instead of genetic differences-- aggression levels increased as more lizards were above ground in groups containing males (mixed-sex and all-male C. sexlineatus groups). The absence of males rather than the genetic relatedness of parthenogenetic whiptail populations affects other social structure characteristics besides behavior in crowded situations (Leuck, MS).

Delineating the effects of phylogeny, genetic relatedness and presence or absence of males on the use of space by whiptail lizards is difficult. But by comparing the behavior of more parthenogenetic and bisexual *Cnemidophorus* species in controlled environments, we may eventually be able to discriminate among ultimate factors affecting species differences in space utilization.

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Table 1. Number of Lizards (of 25 for Each Group) Observed in Burrows under Each Object Available in a 3 m x 3 m x 1 m Enclosure. Enclosure is illustrated in Fig. 2. Use values of each group were compared to an average expected value to generate X^2 values. TRIP TES = triploid *C. tesselatus*, DIP TES = diploid *C. tesselatus*, NEO = *C. neomexicanus*, F SEX = all-female *C. sexlineatus*, MIX SEX = mixed male and female *C. sexlineatus*, M SEX = all-male *C. sexlineatus*.

	TRIP TES	DIP TES	NEO	F SEX	MIX SEX	M SEX
Southwest Block	14	12	9	5	4	1
East Block	7	8	10	3	3	5
Board	13	16	15	7	13	11
Rock 1	6	8	5	1	2	1
Rock 2	2	3	2	2	0	1
Water Bowl	8	2	0	2	3	1
Open Sand	16	16	3	3	4	6
Wall	21	5	6	6	10	4
Average expected use value	10.88	8.75	6.25	3.63	4.88	3.75
X^2 for obs. vs. exp. values	24.67*	23.81*	17.31*	8.86	18.88*	23.56*

* Significant at $P < 0.05$.

Table 2. Use by Lizards of Objects or Areas for Burrowing When Objects Were in an Enclosure and after They Were Removed. Enclosure is illustrated in Fig. 2. "Total" column is the total number of times lizards of each group were observed burrowing when objects were present (OP) or absent (OA). Numbers in rows following each total are percentages of the total value. Abbreviations are in same as in Table 1.

		Total	Block, Rock & Board*	Bowl	Open Sand	Wall
TRIP TES	OP	66	62	9	9	20
	OA	31	16**	7	35	42
DIP TES	OP	49	92	2	2	4
	OA	24	8	8	67	17
NEO	OP	39	92	3	3	2
	OA	17	29	18	18	35
F SEX	OP	21	71	10	5	14
	OA	9	45	0	22	33
MIX SEX	OP	27	74	7	4	15
	OA	15	27	13	20	40
M SEX	OP	25	72	4	16	8
	OA	6	17	0	33	50

* Removed after 14 periods.

** In same location as object was before removal.

Table 3. Number of Lizards (of 25 for Each Group) Burrowing Under One to Two Objects Compared to Number of Lizards Burrowing Under Three to Six Objects. Abbreviations are the same as in Table 1.

	One to Two Objects	Three to Six Objects
Parthenogenetic		
TRIP TES	6	19
DIP TES	11	14
NEO	13	10
TOTAL	30 (41%)*	43 (59%)*
Bisexual		
F SEX	19	1
MIX SEX	21	2
M SEX	19	1
TOTAL	59 (94%)	4 (6%)

* Percentages compared using a 2 x 2 test of independence; G = 46.68 ($P < 0.05$).

FIGURE TITLES

Fig. 1. Relationships of some hybrid all-female *Cnemidophorus* species to their bisexual parental species. Names of species used in this study are shown in boxes.

Fig. 2. Placement of objects in the 3 m x 3 m x 1 m enclosures used for observations.

Fig. 3. Number of times lizards were observed above ground during seven time periods from June - September 1977-1979. TRIP TES = triploid *C. tesselatus*, DIP TES = diploid *C. tesselatus*, NEO = *C. neomexicanus*, F SEX = all-female *C. sexlineatus*, MIX SEX = mixed male and female *C. sexlineatus*, M SEX = all-male *C. sexlineatus*. Parthenogenetic groups are shown in boxes.

Fig. 4. Relation of aggression per lizard-period (see text) to number of lizards above ground in six whiptail lizard groups. Five replicates of five lizards each were observed for each group. Abbreviations are the same as for Fig. 3.

Figure 1

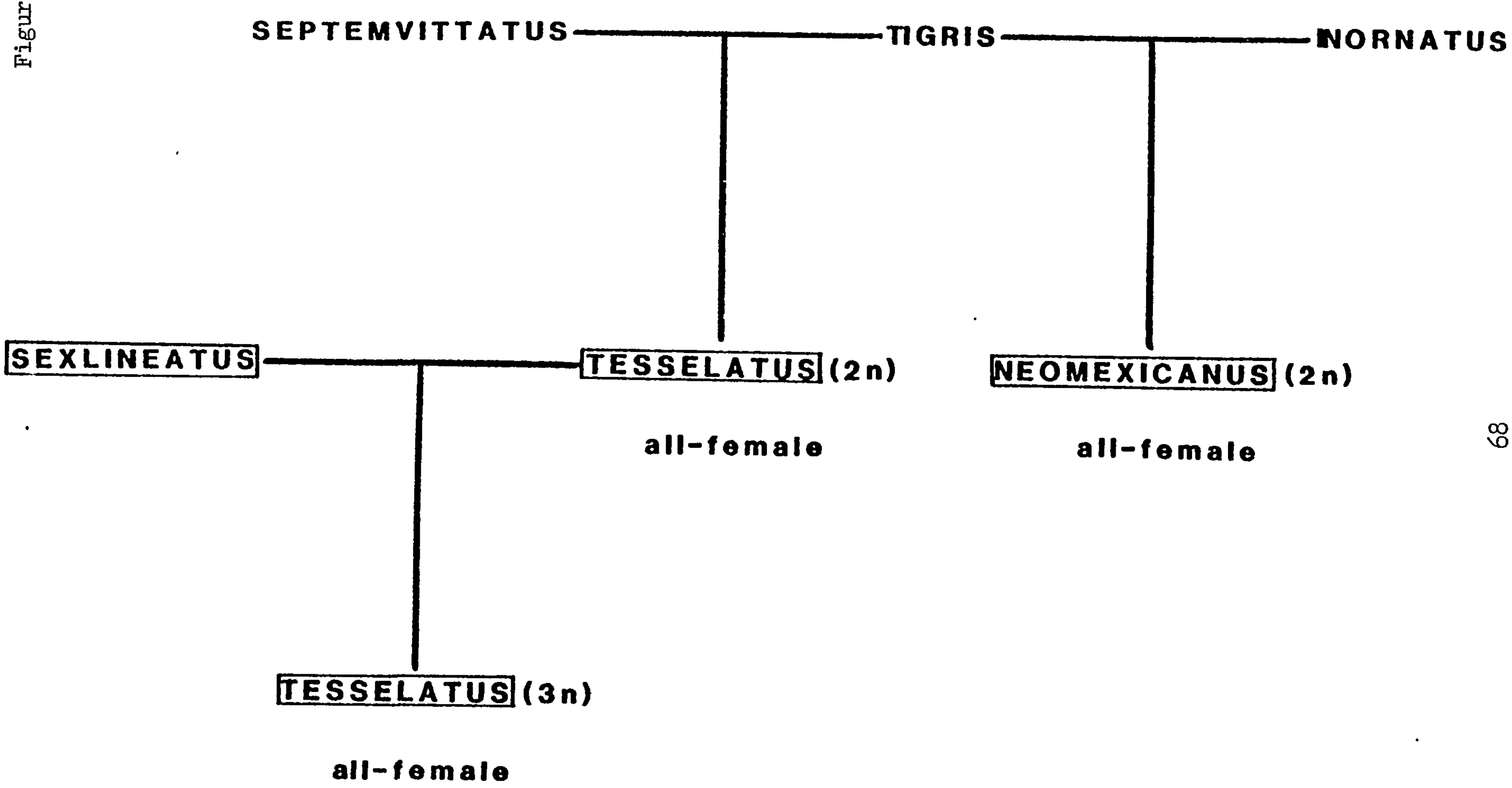

SEPTEMVITTATUS
TIGRIS
INORNATUS
SEXLINEATUS
TESSELATUS (2n)
all-female
NEOMEXICANUS (2n)
all-female
TESSELATUS (3n)
all-female

Figure 2

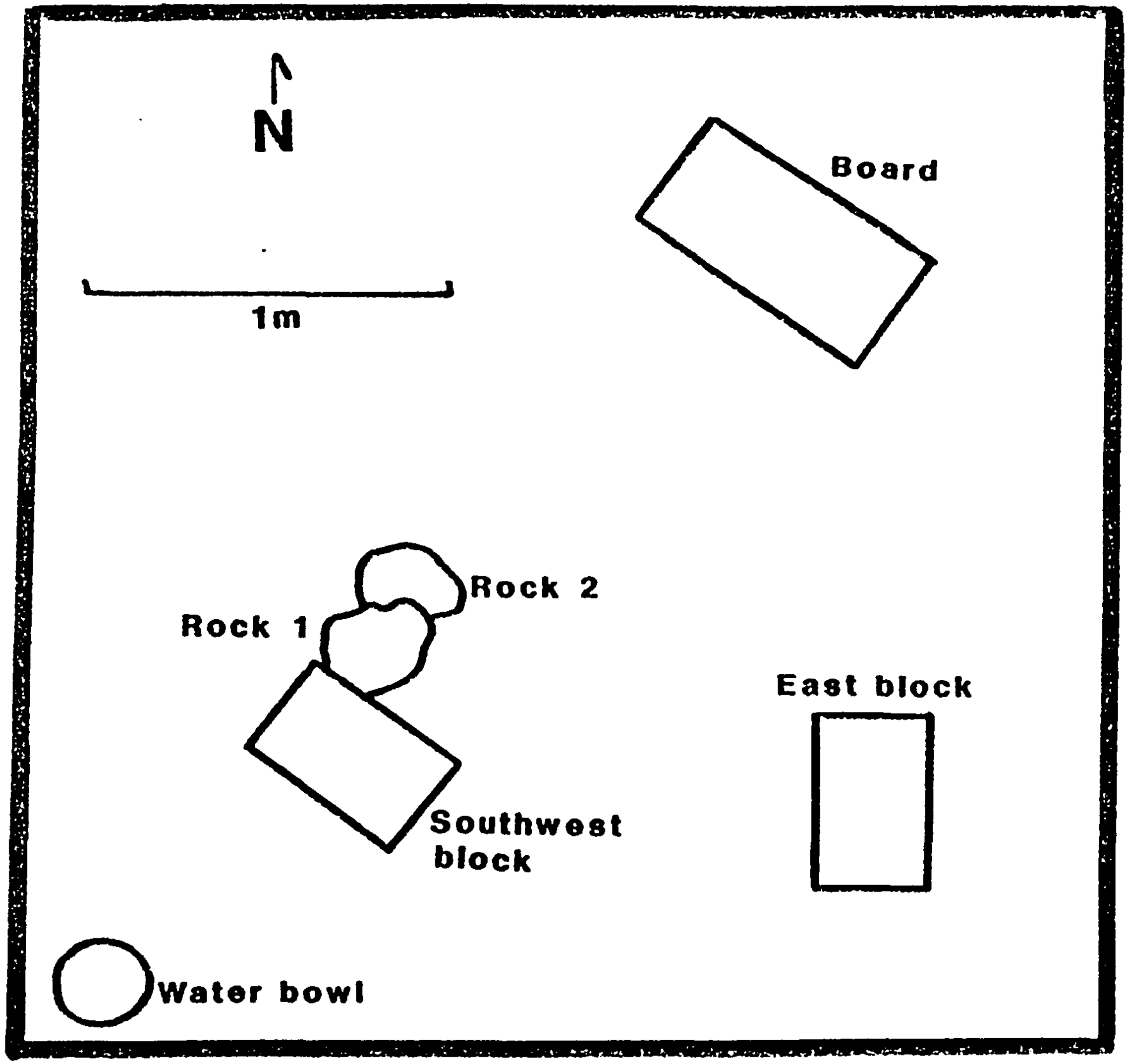

N
1m
Board
Rock 2
Rock 1
East block
Southwest block
Water bowl

Figure 3

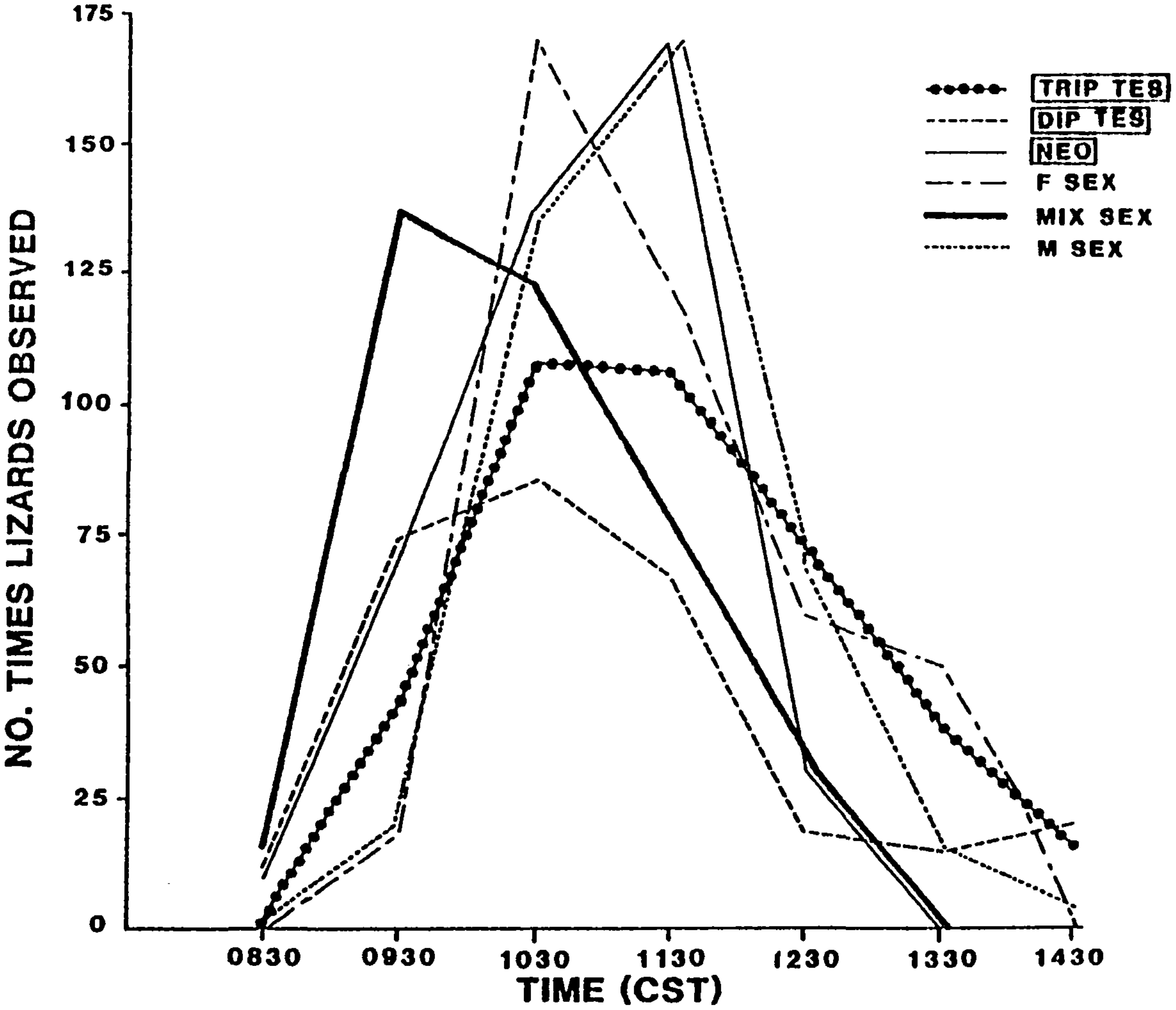
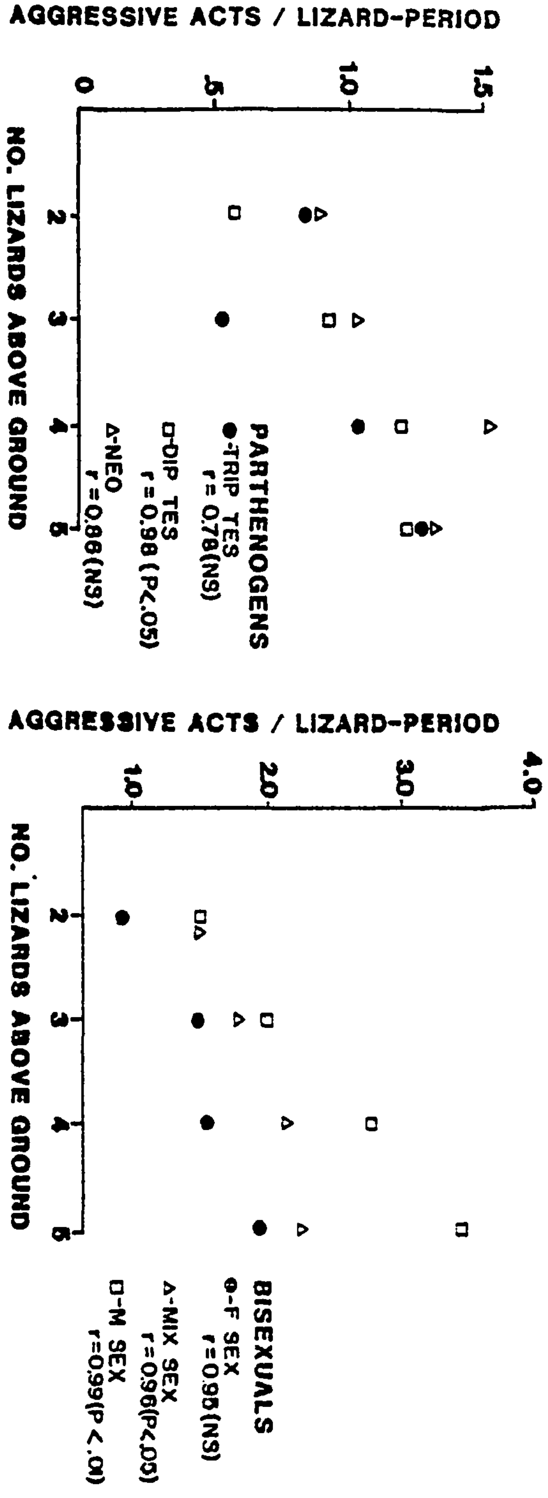

TRIP TES
DIP TES
NEO
F SEX
MIX SEX
M SEX
NO. TIMES LIZARDS OBSERVED
175
150
125
100
75
50
25
0
0830
0930
1030
1130
1230
1330
1430
TIME (CST)

Figure 4


AGGRESSIVE ACTS / LIZARD-PERIOD
0
.5
1.0
1.5
2
3
4
5
NO. LIZARDS ABOVE GROUND
PARTHENOGENS
●-TRIP TES
r= 0.78(NS)
□-DIP TES
r = 0.98 (P<.05)
Δ-NEO
r = 0.88(NS)
AGGRESSIVE ACTS / LIZARD-PERIOD
1.0
2.0
3.0
4.0
2
3
4
5
NO. LIZARDS ABOVE GROUND
BISEXUALS
●-F SEX
r=0.95(NS)
Δ-MIX SEX
r=0.96(P<.05)
□-M SEX
r=0.99(P<.01)

Appendix A. Aggression data for six groups (three species) of lizards (genus Cnemidophorus); five replicates of five lizards in each group. Treatment 1 = first seven 20-min periods; cover in enclosures; no crickets introduced. Treatment 2 = second seven periods; cover in enclosures; two crickets introduced per period. Treatment 3 = last six periods; cover removed; no crickets introduced. Lizard-periods = sum of the number of lizards above ground during each period in a treatment.

Treatment	Supplanting	Chasing	Biting	Lizard-periods
TRIPLOID *C. TESSELATUS*				
REPLICATE 1.				
1	13	0	0	23
2	25	5	0	28
3	30	1	0	24
REPLICATE 2.				
1	38	1	0	32
2	39	0	0	29
3	22	1	0	21
REPLICATE 3.				
1	13	0	0	18
2	27	1	0	30
3	21	0	0	23
REPLICATE 4.				
1	19	0	0	29

Appendix A. continued.

Treatment	Supplanting	Chasing	Biting	Lizard-periods
2	32	0	0	29
3	32	0	0	24
REPLICATE 5.				
1	30	1	2	31
2	34	4	1	30
3	14	0	0	18
DIPLOID *C. TESSELATUS*				
REPLICATE 1.				
1	16	0	0	25
2	9	1	0	16
3	3	0	0	11
REPLICATE 2.				
1	12	1	0	23
2	32	13	1	25
3	37	1	1	25
REPLICATE 3.				
1	4	2	0	20
2	27	1	0	23
3	1	0	0	15
REPLICATE 4.				
1	14	0	1	22

Appendix A. continued.

Treatment	Supplanting	Chasing	Biting	Lizard-periods
2	23	11	2	20
3	8	0	0	12
REPLICATE 5.				
1	11	1	0	17
2	7	15	6	20
3	13	0	1	15
C. NEOMEXICANUS				
REPLICATE 1.				
1	41	0	0	29
2	22	6	3	28
3	36	3	2	25
REPLICATE 2.				
1	18	0	0	27
2	19	0	4	25
3	47	3	0	23
REPLICATE 3.				
1	14	0	0	28
2	26	4	3	28
3	25	0	0	19
REPLICATE 4.				
1	51	0	2	33
2	40	2	2	32

Appendix A. continued.

Treatment	Supplanting	Chasing	Biting	Lizard-periods
3	47	0	1	26
REPLICATE 5.				
1	47	0	2	32
2	44	14	7	33
3	39	1	1	27
ALL-FEMALE <u>C</u>. <u>SEXLINEATUS</u>				
REPLICATE 1.				
1	24	8	5	28
2	23	16	6	29
3	36	4	2	29
REPLICATE 2.				
1	21	5	0	25
2	20	5	3	25
3	28	4	2	21
REPLICATE 3.				
1	36	0	3	30
2	39	6	8	30
3	52	1	1	26
REPLICATE 4.				
1	42	10	8	29
2	34	9	5	26

Appendix A. continued.

Treatment	Supplanting	Chasing	Biting	Lizard-periods
3	61	7	5	28
REPLICATE 5.				
1	56	3	1	35
2	22	17	9	27
3	17	2	1	20
MIXED-SEX *C. SEXLINEATUS*				
REPLICATE 1.				
1	46	32	17	31
2	32	17	10	31
3	17	6	3	19
REPLICATE 2.				
1	26	2	2	29
2	20	14	2	30
3	20	5	2	28
REPLICATE 3.				
1	34	0	2	29
2	20	5	0	29
3	23	3	0	24
REPLICATE 4.				
1	44	31	16	29
2	28	24	9	28

Appendix A. continued.

Treatment	Supplanting	Chasing	Biting	Lizard-periods
3	45	26	16	22
REPLICATE 5.				
1	91	13	6	29
2	54	15	5	30
3	99	14	5	27
ALL-MALE *C. SEXLINEATUS*				
REPLICATE 1.				
1	40	14	5	23
2	15	22	3	24
3	35	4	1	22
REPLICATE 2.				
1	37	5	2	28
2	23	16	5	29
3	41	32	7	27
REPLICATE 3.				
1	72	14	4	34
2	108	21	7	32
3	51	8	3	25
REPLICATE 4.				
1	80	20	3	29
2	123	23	15	31

Appendix A. continued.

Treatment	Supplanting	Chasing	Biting	Lizard-periods
3	124	10	4	26
REPLICATE 5.				
1	54	7	3	30
2	52	6	2	29
3	85	6	1	22

Appendix B. Snout-vent length, sex, number of other lizards dominated (rank), periods out and number of crickets eaten for each lizard of six groups (three species of Cnemidophorus); five replicates of five lizards in each group. Combinations of letters and numbers in the first column refer to individual lizards in each replicate.

	S-V length	Sex	Rank	Periods out	Crickets eaten
TRIPLOID C. TESSELATUS					
REPLICATE 1.					
R1S	89mm	F	4	18	3
R2S	83mm	F	2	13	4
R3S	79mm	F	1	14	1
H1S	76mm	F	1	17	1
H2S	79mm	F	1	13	4
REPLICATE 2.					
R1S	81mm	F	0	10	2
R2S	83mm	F	2	18	2
R3S	86mm	F	1	19	3
H1S	88mm	F	3	18	4
H2S	87mm	F	2	16	2
REPLICATE 3.					
R1S	75mm	F	0	18	0
R2S	77mm	F	2	14	0
R3S	78mm	F	2	12	6
H1S	80mm	F	4	13	1
H2S	77mm	F	1	13	1

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
REPLICATE 4.					
R1S	72mm	F	1	17	3
R2S	72mm	F	1	15	2
R3S	73mm	F	0	13	2
H1S	76mm	F	3	17	3
H2S	79mm	F	4	19	1
REPLICATE 5.					
R1S	73mm	F	0	17	0
R2S	74mm	F	4	15	0
R3S	75mm	F	1	16	0
H1S	75mm	F	1	15	4
H2S	89mm	F	3	15	8
DIPLOID _C_. _TESSELATUS_					
REPLICATE 1.					
R1S	79mm	F	1	12	8
R2S	79mm	F	2	11	1
R3S	79mm	F	2	7	0
H1S	76mm	F	1	9	2
H2S	76mm	F	2	11	0
REPLICATE 2.					
R1S	60mm	F	3	17	4
R2S	57mm	F	0	16	1

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
R3S	67mm	F	1	11	2
H1S	64mm	F	3	16	3
H2S	76mm	F	3	11	1
REPLICATE 3.					
R1S	79mm	F	0	14	2
R2S	76mm	F	2	15	5
R3S	79mm	F	2	13	6
H1S	76mm	F	1	7	1
H2S	83mm	F	1	7	0
REPLICATE 4.					
R1S	87mm	F	2	17	4
R2S	80mm	F	0	10	2
R3S	78mm	F	1	15	2
H1S	79mm	F	1	18	4
H2S	80mm	F	2	4	0
REPLICATE 5.					
R1S	80mm	F	1	14	3
R2S	82mm	F	0	1	0
R3S	77mm	F	1	12	4
H1S	75mm	F	1	12	1
H2S	81mm	F	3	14	4

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
C. NEOMEXICANUS					
REPLICATE 1.					
R1S	63mm	F	0	18	3
R2S	66mm	F	0	12	2
R3S	68mm	F	3	13	2
H1S	65mm	F	2	20	6
H2S	72mm	F	4	18	0
REPLICATE 2.					
R1S	64mm	F	2	13	3
R2S	65mm	F	0	16	2
R3S	70mm	F	3	13	2
H1S	64mm	F	1	19	5
H2S	68mm	F	3	15	3
REPLICATE 3.					
R1S	64mm	F	2	18	3
R2S	62mm	F	0	19	2
R3S	67mm	F	0	10	1
H1S	68mm	F	2	15	4
H2S	73mm	F	3	15	3
REPLICATE 4.					
R1S	66mm	F	0	19	2
R2S	67mm	F	1	18	3

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
R3S	76mm	F	4	19	2
H1S	72mm	F	2	15	5
H2S	74mm	F	3	19	1
REPLICATE 5.					
R1S	72mm	F	2	18	4
R2S	71mm	F	3	19	3
R3S	74mm	F	3	20	3
H1S	72mm	F	2	19	4
H2S	73mm	F	1	16	3
ALL-FEMALE *C. SEXLINEATUS*					
REPLICATE 1.					
R1S	54mm	F	1	18	3
R2S	54mm	F	0	15	4
R3S	53mm	F	0	14	2
H1S	59mm	F	4	18	2
H2S	60mm	F	3	20	2
REPLICATE 2.					
R1S	60mm	F	3	18	5
R2S	57mm	F	1	20	2
R3S	60mm	F	1	9	1
H1S	62mm	F	1	10	0
H2S	61mm	F	3	15	4

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
REPLICATE 3.					
R1S	50mm	F	0	18	2
R2S	49mm	F	2	20	1
R3S	58mm	F	1	19	5
H1S	59mm	F	2	19	2
H2S	60mm	F	4	19	4
REPLICATE 4.					
R1S	59mm	F	1	20	3
R2S	57mm	F	0	17	4
R3S	56mm	F	2	19	2
H1S	58mm	F	4	17	4
H2S	60mm	F	3	9	1
REPLICATE 5.					
R1S	55mm	F	0	13	1
R2S	57mm	F	1	19	2
R3S	57mm	F	2	12	3
H1S	56mm	F	2	18	4
H2S	57mm	F	4	20	4
MIXED-SEX *C. SEXLINEATUS*					
REPLICATE 1.					
R1S	55mm	F	0	17	1
R2S	56mm	M	4	19	3

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
R3S	55mm	M	2	18	3
H1S	61mm	M	1	15	1
H2S	60mm	F	1	11	3
REPLICATE 2.					
R1S	60mm	F	1	17	3
R2S	51mm	F	0	14	2
R3S	52mm	M	2	17	3
H1S	59mm	M	3	19	2
H2S	59mm	M	4	20	2
REPLICATE 3.					
R1S	56mm	F	3	18	2
R2S	53mm	F	1	17	3
R3S	57mm	F	0	11	3
H1S	55mm	M	2	18	4
H2S	58mm	M	4	18	2
REPLICATE 4.					
R1S	49mm	F	1	19	0
R2S	49mm	M	0	5	0
R3S	60mm	M	3	19	3
H1S	61mm	M	4	19	6
H2S	62mm	F	2	16	3

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
REPLICATE 5.					
R1S	60mm	F	0	11	2
R2S	58mm	F	1	19	5
R3S	60mm	F	2	17	2
H1S	64mm	M	3	19	2
H2S	63mm	M	4	20	2
ALL-MALE <u>C</u>. <u>SEXLINEATUS</u>					
REPLICATE 1.					
R1S	55mm	M	0	15	3
R2S	58mm	M	2	17	2
R3S	53mm	M	1	18	5
H1S	59mm	M	4	13	1
H2S	60mm	M	3	5	2
REPLICATE 2.					
R1S	51mm	M	0	18	3
R2S	58mm	M	4	14	1
R3S	57mm	M	3	19	3
H1S	60mm	M	1	18	2
H2S	62mm	M	2	14	5
REPLICATE 3.					
R1S	54mm	M	0	17	2
R2S	55mm	M	1	20	2

Appendix B. continued.

	S-V length	Sex	Rank	Periods out	Crickets eaten
R3S	62mm	M	3	20	4
H1S	60mm	M	4	19	2
H2S	63mm	M	2	18	4
REPLICATE 4.					
R1S	56mm	M	1	19	0
R2S	59mm	M	0	12	2
R3S	60mm	M	3	20	4
H1S	62mm	M	2	18	3
H2S	60mm	M	4	17	4
REPLICATE 5.					
R1S	56mm	M	2	13	3
R2S	57mm	M	0	15	3
R3S	56mm	M	1	13	0
H1S	62mm	M	3	20	6
H2S	61mm	M	4	19	2

Appendix C. Dominance relationships in each replicate. Combinations of letters and numbers refer to individual lizards in each replicate. Winners of aggressive interactions (supplanting + chasing + biting) are listed on the left side and losers are listed across the top of each matrix.

TRIPLOID *C. TESSELATUS*

REPLICATE 1.

	R1S	R2S	R3S	H1S	H2S
R1S		8	4	6	11
R2S	3		1	3	6
R3S	0	2		1	1
H1S	0	1	2		4
H2S	3	4	1	8	

REPLICATE 2.

	R1S	R2S	R3S	H1S	H2S
R1S		4	2	5	1
R2S	5		4	9	2
R3S	2	6		3	2
H1S	6	12	14		7
H2S	2	0	7	7	

REPLICATE 3.

	R1S	R2S	R3S	H1S	H2S
R1S		2	2	0	4
R2S	5		2	5	5
R3S	4	2		3	2
H1S	6	8	5		3
H2S	3	0	0	1	

REPLICATE 4.

	R1S	R2S	R3S	H1S	H2S
R1S		7	3	6	4
R2S	4		5	1	2
R3S	3	0		3	2
H1S	8	7	4		3
H2S	6	6	5	4	

REPLICATE 5.

	R1S	R2S	R3S	H1S	H2S
R1S		2	3	3	2
R2S	7		5	5	6
R3S	4	2		1	4
H1S	6	2	1		3
H2S	4	5	6	11	

Appendix C. continued.

DIPLOID *C. TESSELATUS*

REPLICATE 1.

	R1S	R2S	R3S	H1S	H2S
R1S		1	0	3	1
R2S	2		1	1	0
R3S	7	1		2	1
H1S	0	0	1		1
H2S	2	2	1	0	

REPLICATE 2.

	R1S	R2S	R3S	H1S	H2S
R1S		13	4	2	7
R2S	10		1	4	3
R3S	2	3		3	0
H1S	7	7	6		2
H2S	2	4	6	7	

REPLICATE 3.

	R1S	R2S	R3S	H1S	H2S
R1S		1	0	0	0
R2S	3		3	2	2
R3S	6	8		1	0
H1S	0	0	2		0
H2S	0	2	2	0	

REPLICATE 4.

	R1S	R2S	R3S	H1S	H2S
R1S		2	6	8	2
R2S	1		3	1	0
R3S	5	6		1	2
H1S	8	3	1		0
H2S	2	1	4	0	

REPLICATE 5.

	R1S	R2S	R3S	H1S	H2S
R1S		0	2	4	2
R2S	0		0	0	0
R3S	3	0		0	2
H1S	1	0	2		4
H2S	7	0	10	10	

Appendix C. continued.

C. NEOMEXICANUS

REPLICATE 1.

	R1S	R2S	R3S	H1S	H2S
R1S		1	2	5	5
R2S	1		0	1	1
R3S	3	2		5	1
H1S	8	12	4		12
H2S	14	6	8	17	

REPLICATE 2.

	R1S	R2S	R3S	H1S	H2S
R1S		10	3	8	1
R2S	3		1	3	1
R3S	4	1		6	3
H1S	4	6	3		4
H2S	5	9	1	12	

REPLICATE 3.

	R1S	R2S	R3S	H1S	H2S
R1S		5	0	1	8
R2S	2		4	9	6
R3S	0	4		1	1
H1S	1	10	2		2
H2S	0	8	2	3	

REPLICATE 4.

	R1S	R2S	R3S	H1S	H2S
R1S		6	3	3	0
R2S	8		1	4	1
R3S	17	8		12	13
H1S	7	7	8		10
H2S	6	15	4	12	

REPLICATE 5.

	R1S	R2S	R3S	H1S	H2S
R1S		2	3	7	10
R2S	11		1	4	1
R3S	14	8		12	13
H1S	6	7	8		10
H2S	9	15	4	12	

Appendix C. continued.

ALL-FEMALE *C. SEXLINEATUS*

REPLICATE 1.

	R1S	R2S	R3S	H1S	H2S
R1S		3	2	4	4
R2S	1		4	1	1
R3S	2	4		7	2
H1S	11	6	9		20
H2S	5	4	6	15	

REPLICATE 2.

	R1S	R2S	R3S	H1S	H2S
R1S		12	0	3	5
R2S	6		1	9	7
R3S	0	3		0	2
H1S	1	4	0		8
H2S	4	10	3	4	

REPLICATE 3.

	R1S	R2S	R3S	H1S	H2S
R1S		3	2	0	1
R2S	18		15	2	9
R3S	12	6		2	4
H1S	3	2	3		5
H2S	19	15	15	10	

REPLICATE 4.

	R1S	R2S	R3S	H1S	H2S
R1S		18	9	2	1
R2S	11		4	4	3
R3S	11	7		2	5
H1S	24	16	19		11
H2S	15	6	6	7	

REPLICATE 5.

	R1S	R2S	R3S	H1S	H2S
R1S		2	0	1	1
R2S	12		4	4	3
R3S	3	7		2	5
H1S	19	16	19		11
H2S	5	6	6	7	

Appendix C. continued.

MIXED-SEX <u>C</u>. <u>SEXLINEATUS</u>

REPLICATE 1.

	R1S	R2S	R3S	H1S	H2S
R1S		0	4	0	0
R2S	21		41	38	14
R3S	9	1		6	3
H1S	1	1	4		1
H2S	0	0	5	1	

REPLICATE 2.

	R1S	R2S	R3S	H1S	H2S
R1S		4	1	2	2
R2S	1		0	0	0
R3S	6	7		4	1
H1S	4	6	5		7
H2S	10	9	3	16	

REPLICATE 3.

	R1S	R2S	R3S	H1S	H2S
R1S		12	2	9	1
R2S	8		6	3	0
R3S	0	4		1	0
H1S	7	5	2		2
H2S	7	7	3	7	

REPLICATE 4.

	R1S	R2S	R3S	H1S	H2S
R1S		3	0	0	1
R2S	1		0	0	0
R3S	30	3		7	9
H1S	39	6	10		13
H2S	14	1	14	18	

REPLICATE 5.

	R1S	R2S	R3S	H1S	H2S
R1S		4	6	0	4
R2S	5		10	2	1
R3S	17	60		12	7
H1S	7	26	28		18
H2S	10	36	25	24	

Appendix C. continued.

ALL-MALE *C. SEXLINEATUS*

REPLICATE 1.

	R1S	R2S	R3S	H1S	H2S
R1S		3	8	1	1
R2S	22		14	2	1
R3S	11	6		4	0
H1S	9	7	21		2
H2S	2	10	6	0	

REPLICATE 2.

	R1S	R2S	R3S	H1S	H2S
R1S		0	1	4	4
R2S	15		14	13	6
R3S	19	7		11	6
H1S	15	3	6		5
H2S	11	4	3	6	

REPLICATE 3.

	R1S	R2S	R3S	H1S	H2S
R1S		8	2	2	3
R2S	18		5	3	12
R3S	12	25		13	18
H1S	24	24	31		37
H2S	16	20	8	5	

REPLICATE 4.

	R1S	R2S	R3S	H1S	H2S
R1S		38	15	15	1
R2S	1		2	1	0
R3S	27	22		18	3
H1S	20	17	7		0
H2S	94	29	40	49	

REPLICATE 5.

	R1S	R2S	R3S	H1S	H2S
R1S		16	10	3	2
R2S	4		2	6	2
R3S	7	4		8	0
H1S	17	14	25		4
H2S	23	22	20	30	

Appendix D. Number of lizards (of 25 in each of six groups; three species) using burrows under each available object in 3m x 3m enclosures.

	Southwest block	East block	Board	Rock 1	Rock 2	Bowl	Open sand	Against wall
TRIPLOID *C. TESSELATUS*								
	14	7	13	6	2	8	16	21
DIPLOID *C. TESSELATUS*								
	12	8	16	8	3	2	16	5
C. NEOMEXICANUS								
	9	10	15	5	2	0	3	6
ALL-FEMALE *C. SEXLINEATUS*								
	5	3	7	1	2	2	3	6
MIXED-SEX *C. SEXLINEATUS*								
	4	3	13	2	0	3	4	10
ALL-MALE *C. SEXLINEATUS*								
	1	5	11	1	2	1	7	3

Appendix E. Number of lizards in each rank category listed by number of objects under which they burrowed (out of eight possible objects in 3m x 3m enclosures).

TRIPLOID	Rank	Number of objects:							
C. *TESSELATUS*		1	2	3	4	5	6	7	8
	0	0	1	3	0	1	0	0	0
	1	0	2	1	1	4	0	0	0
	2	1	1	1	2	0	0	0	0
	3	1	0	1	0	0	1	0	0
	4	0	0	1	2	1	0	0	0
DIPLOID	0	1	2	0	1	0	0	0	0
C. *TESSELATUS*	1	1	3	3	3	0	0	0	0
	2	0	3	3	1	0	0	0	0
	3	0	1	1	1	1	0	0	0
	4	0	0	0	0	0	0	0	0
C. *NEOMEXICANUS*	0	2	1	2	1	0	0	0	0
	1	0	2	1	1	0	0	0	0
	2	3	1	0	1	0	0	0	0
	3	3	1	3	0	0	0	0	0
	4	0	0	1	0	0	0	0	0
ALL-FEMALE	0	3	1	0	0	0	0	0	0
C. *SEXLINEATUS*	1	2	3	1	0	0	0	0	0
	2	2	2	0	0	0	0	0	0
	3	2	1	0	0	0	0	0	0
	4	3	0	0	0	0	0	0	0

Appendix E. continued.

	Rank	Number of objects:							
		1	2	3	4	5	6	7	8
MIXED-SEX	0	3	2	0	0	0	0	0	0
C. SEXLINEATUS	1	2	2	0	0	1	0	0	0
	2	4	1	0	0	0	0	0	0
	3	1	1	1	0	0	0	0	0
	4	1	4	0	0	0	0	0	0
ALL-MALE	0	1	1	0	0	0	0	0	0
C. SEXLINEATUS	1	1	3	0	0	0	0	0	0
	2	3	2	0	0	0	0	0	0
	3	3	1	0	0	0	0	0	0
	4	3	1	1	0	0	0	0	0

Appendix F. Number of times lizards were observed during seven time periods. A lizard was recorded as observed each time it was above ground during a period. Time period I = 830-930 (Central Standard Time); II = 930-1030 hr; III = 1030-1130 hr; IV = 1130-1230 hr; V = 1230-1330 hr; VI = 1330-1430 hr; VII = 1430-1530 hr.

	Time period:						
	I	II	III	IV	V	VI	VII
TRIPLOID							
C. TESSELATUS	1	43	109	107	72	38	14
DIPLOID							
C. TESSELATUS	11	74	86	66	18	12	21
C. NEOMEXICANUS	10	74	135	165	30	0	0
ALL-FEMALE							
C. SEXLINEATUS	0	16	166	122	60	50	0
MIXED-SEX							
C. SEXLINEATUS	17	135	122	75	29	0	0
ALL-MALE							
C. SEXLINEATUS	0	21	133	166	70	15	4

Appendix G. Dates on which each of five replicates of six groups of lizards (three species) was observed. Number of periods for which each replicate was observed on a given date and high temperature for the date are also listed. Temperatures (^{o}C) were obtained from the Severe Storms Laboratory, U.S. Department of Commerce, Max Westheimer Airfield, Norman, Oklahoma (approximately 1 km from observation site).

Date	Periods	Temperature	Date	Periods	Temperature
TRIPLOID *C. TESSELATUS*					
REPLICATE 1.			REPLICATE 2.		
7/7/77	3	36	8/21/77	2	31.5
7/9/77	4	34	8/22/77	5	33
7/13/77	4	37.5	8/24/77	2	37.5
7/14/77	3	37.5	8/25/77	5	37
7/20/77	3	38	9/3/77	1	34
7/21/77	2	35.5	9/4/77	5	35
7/25/77	1	41			
REPLICATE 3.			REPLICATE 4.		
8/21/77	2	31.5	9/6/77	3	31
8/22/77	5	33	9/8/77	3	33
8/24/77	2	37.5	9/10/77	1	32
8/25/77	5	37	9/11/77	3	35.5
9/3/77	2	34	9/17/77	4	33
9/4/77	4	35	9/18/77	4	35
			9/20/77	2	31.5

Appendix G. continued.

REPLICATE 5.

Date	Periods	Temperature
9/6/77	3	31
9/8/77	3	33
9/10/77	1	32
9/11/77	4	35.5
9/17/77	3	33
9/18/77	4	35
9/20/77	2	31.5

DIPLOID *C. TESSELATUS*

REPLICATE 1.

Date	Periods	Temperature
7/7/77	2	36
7/10/77	5	36
7/13/77	2	37.5
7/14/77	3	37
7/16/77	2	37.5
7/20/77	1	38
7/21/77	4	35.5
7/25/77	1	41

REPLICATE 2.

Date	Periods	Temperature
7/16/77	2	37.5
7/17/77	3	36.5
7/18/77	2	37
7/23/77	2	38
7/24/77	5	40
7/25/77	1	40
7/28/77	5	--

REPLICATE 3.

Date	Periods	Temperature
7/16/77	2	37.5
7/17/77	3	36.5
7/18/77	2	37
7/23/77	4	38
7/24/77	3	40
7/25/77	4	41
7/28/77	2	--

REPLICATE 4.

Date	Periods	Temperature
8/22/77	1	33
8/23/77	4	37.5
8/24/77	2	37.5
8/26/77	4	37

REPLICATE 5.

Date	Periods	Temperature
8/23/77	4	37.5
8/24/77	3	37.5
8/26/77	4	37
8/27/77	3	35.5

Appendix G. continued.

Date	Periods	Temperature	Date	Periods	Temperature
8/27/77	3	35.5	8/30/77	1	33
8/30/77	2	33	9/1/77	3	33
9/1/77	1	33	9/3/77	2	34
9/3/77	3	34			

C. NEOMEXICANUS

REPLICATE 1.			REPLICATE 2.		
6/14/78	3	31.5	6/14/78	3	31.5
6/15/78	4	33	6/15/78	2	33
6/16/78	2	32	6/16/78	1	32
6/20/78	1	33	6/20/78	4	33
6/25/78	1	35	6/25/78	4	35
6/27/78	3	32.5	6/27/78	2	32.5
6/28/78	6	33	6/28/78	3	33

REPLICATE 3.			REPLICATE 4.		
7/3/78	2	37	6/23/79	2	32
7/4/78	4	36.5	6/26/79	5	29
7/5/78	1	37	6/27/79	4	31
7/11/78	4	38	6/28/79	1	33.5
7/17/78	5	37.5	6/29/79	2	35
7/18/78	2	40	7/1/79	4	36
7/19/78	2	39	7/2/79	2	34

Appendix G. continued.

REPLICATE 5.

Date	Periods	Temperature
7/2/79	5	34
7/3/79	4	34
7/4/79	2	36
7/13/79	3	34.5
7/14/79	2	34.5
7/15/79	2	34.5
7/21/79	2	31

ALL-FEMALE *C.* SEXLINEATUS

REPLICATE 1.

Date	Periods	Temperature
7/27/78	4	33
7/28/78	1	36.5
7/29/78	1	37
7/30/78	3	39
8/9/78	1	34
8/10/78	1	32
8/11/78	3	36.5
8/14/78	3	37
8/15/78	3	35

REPLICATE 2.

Date	Periods	Temperature
7/28/78	3	36.5
7/29/78	1	37
7/30/78	4	39
8/10/78	3	32
8/11/78	3	36.5
8/14/78	3	37
8/15/78	3	35

REPLICATE 3.

Date	Periods	Temperature
7/21/79	6	31
7/23/79	2	--
7/26/79	2	31
7/27/79	4	--
7/28/79	4	35
7/29/79	2	35

REPLICATE 4.

Date	Periods	Temperature
7/22/79	2	32
7/26/79	1	31
7/28/79	3	35

REPLICATE 5.

Date	Periods	Temperature
8/2/79	5	32
8/3/79	3	33.5
8/4/79	1	34.5

Appendix G. continued.

Date	Periods	Temperature
7/29/79	2	35
7/30/79	1	35.5
7/31/79	2	30
8/1/79	1	31
8/2/79	2	32
8/3/79	1	33.5
8/4/79	3	34.5
8/5/79	2	35

Date	Periods	Temperature
8/5/79	2	35
8/6/79	2	36.5
8/7/79	1	36
8/8/79	3	34
8/11/79	3	27.5

MIXED-SEX *C. SEXLINEATUS*

REPLICATE 1.

7/3/78	7	37
7/4/78	2	36.5
7/5/78	3	37
7/13/78	2	40
7/14/78	1	40
7/17/78	1	37.5
7/18/78	2	40
7/19/78	2	39

REPLICATE 3.

7/10/78	3	39
7/11/78	1	38
7/12/78	3	37.5
7/13/78	2	40

REPLICATE 2.

7/10/78	4	39
7/11/78	2	38
7/12/78	1	37.5
7/14/78	2	40
7/15/78	3	37.5
7/17/78	2	37.5
7/18/78	1	40
7/19/78	2	39
7/20/78	3	37

REPLICATE 4.

6/29/79	1	35
7/1/79	5	36
7/2/79	2	34

Appendix G. continued.

Date	Periods	Temperature
7/14/78	3	40
7/15/78	2	37.5
7/18/78	2	40
7/19/78	1	39
7/20/78	3	37

Date	Periods	Temperature
7/3/79	3	34
7/4/79	1	36
7/13/79	1	34.5
7/14/79	1	34.5
7/15/79	2	34.5
7/20/79	4	30

REPLICATE 5.

7/22/79	2	32
7/26/79	2	31
7/28/79	1	35
7/29/79	3	35
7/30/79	2	35.5
7/31/79	1	30
8/1/79	2	31
8/2/79	2	32
8/3/79	1	33.5
8/4/79	3	34.5
8/5/79	1	35

ALL-MALE *C. SEXLINEATUS*

REPLICATE 1.

7/22/78	1	35.5
7/25/78	7	36.5
7/26/78	3	40
7/27/78	3	33
7/28/78	4	36.5
7/29/78	2	36.5

REPLICATE 2.

7/22/78	3	35.5
7/25/78	1	36.5
7/26/78	5	40
7/27/78	3	33

REPLICATE 3.

7/11/79	4	33.5
7/12/79	3	34
7/13/79	1	34.5
7/14/79	2	34.5

Appendix G. continued.

Date	Periods	Temperature
7/28/78	3	36.5
7/29/78	5	36.5

REPLICATE 4.

Date	Periods	Temperature
7/11/79	4	33.5
7/12/79	3	34
7/13/79	1	34.5
7/14/79	3	34.5
7/15/79	3	34.5
7/16/79	3	34
7/20/79	1	30
7/21/79	2	31

Date	Periods	Temperature
7/15/79	1	34.5
7/16/79	3	34
7/22/79	2	32
7/24/79	1	32.5
7/26/79	1	31
7/28/79	1	35
7/29/79	1	35

REPLICATE 5.

Date	Periods	Temperature
8/7/79	3	36
8/9/79	2	34
8/10/79	2	36.5
8/11/79	1	27.5
8/12/79	3	27.5
8/13/79	1	34
8/14/79	1	36
8/15/79	1	32.5
8/16/79	2	34
8/17/79	3	33.5
8/18/79	1	35.5