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THE BEHAVIORAL ECOLOGY OF THE VIVIPAROUS LIZARD, SCELOPORUS JARROVI

by

Douglas Early Ruby

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Zoology)
in The University of Michigan
1976

Doctoral Committee:

Professor Donald W. Tinkle, Chairman
Professor Richard D. Alexander
Associate Professor Gary W. Fowler
Assistant Professor Ronald A. Nussbaum

To Sally

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CHAPTER I

INTRODUCTION

Natural selection favors those organisms which compete successfully for limited resources and leave more surviving progeny. Since an animal acquires resources by behavioral means, a strong correlation is expected between behavioral patterns and individual fitness. Every behavior has associated benefits and costs (advantages and disadvantages) which affect the reproductive success (RS) of an individual. By maximizing the benefit /cost ratio, an animal optimizes its reproductive gain. I explored the adaptive value of behavior exhibited by the lizard Sceloporus jarrovi in (1) mating patterns, (2) territoriality, and (3) winter activity.

By behaving appropriately an animal can maximize RS by increasing individual survival and/or by enhancing mating performance or reproductive output. Darwin (1871) attempted to explain male attributes which improved mating success but seemed to reduce survival. In his theory of sexual selection, he suggested two classes of selective factors: 1) male-male competition for females and 2) female choice. He also observed that males attempted to court any female; females, on the other hand, generally resisted the male's attention. These sexual differences in courtship behavior may best be interpreted as the result of selection upon members of each sex to maximize their own reproductive

success (Orians, 1969). In most species, females invest more energy in gametes and have greater confidence in their genetic relationship to the zygote than males. Consequently, females are more careful in their choice of mates and more likely to continue investing in their offspring after mating (Trivers, 1972). Because paternity may be uncertain, males frequently gain by mating promiscuously and investing less in each offspring. Errors by males in judgement of mate quality may cause little loss of fitness. By similar errors of judgement, females may forfeit a complete reproductive period because the resources for another clutch may be inaccessible. Females may mate promiscuously only if maximal genetic diversity within young was advantageous (Williams, 1975) or several matings were necessary to fertilize the entire egg clutch.

Orians (1969) proposed a model relating ecological conditions to mating systems. He suggested polygyny should occur if the paternal contribution was only genes or if territories necessary for raising young were markedly different in quality. In the latter case, females may gain by choosing a male who possesses a good territory and other mates rather than choosing an unmated male on a poor territory. Polygyny is assumed to be always advantageous to males and hence its evolution depends upon the advantages and disadvantages of polygyny to the females (Verner and Willson, 1966). Monogamy should occur in situations where food-gathering by both parents results in the maximal RS for each of them.

Males in a wide variety of organisms display the greater variance in RS predicted by Orians and others (see Trivers, 1972 for review). Determination of reproductive success requires knowledge about the breeding structure of the population: 1) the copulation frequency of individual males, 2) the probability of females mating more than once in a season, 3) the relationship between copulation success and insemination, 4) the probability of offspring survival as a function of the paternal degree of polygyny and 5) the amount of parental care by each sex. A desirable measure of RS would be the per parent number of offspring surviving to sexual maturity. Realized fitness (number of offspring reaching maturity) was used to demonstrate the relationship between female territory size and RS in the lizard Uta stansburiana (Tinkle, 1969a). However, most studies have utilized the number of copulations (Robel, 1966; Robel and Ballard, 1974; Trivers, 1972; LeBouef, 1974 and others) or the number of fledgings (Lack 1954, 1968) for practical considerations on the assumption that such measures will roughly correlate with the number of offspring surviving to sexual maturity. There are no data at present to evaluate the validity of this assumption. A primary goal of this study was measuring RS for individual male Sceloporus jarrovi. I used potential numbers of offspring per adult male, based on size-specific fecundity estimates of females with whom the male mated. This method recognizes differences in value between females from the male viewpoint but

ignores differential post-partum survivorship within and between litters.

Even within a single population, males may utilize different strategies to obtain females. The strategy which produces the greatest RS for the energy, time and risk expended would be the optimal one. A current hypothesis for explaining the observed male strategies is that they result from the temporal and spatial distributions of females (Trivers, 1972; Campanella and Wolf, 1974; Alexander, 1975). Depending upon the predictability with which females can be located, aggression with respect to space may be favored. If females are site restricted in general movements or in ovipositing sites, male defense of such areas may be reproductively advantageous. Variations in the quality of areas may produce greater or lesser degrees of clumping by females. The greater the clumping, the greater the potential variation in male RS. Actual RS would depend upon the male-male competition and the duration of the breeding season. Variation in RS may be low in explosive breeders (for example, frogs; Bragg, 1965) if other males can mate while a dominant individual does. In animals with prolonged breeding seasons, variation in RS may be either high or low depending upon the parental investment by the male. If females do clump, dominance relationship may give one male priority to the females which gather at the site. However, subordinate males may mate while the dominant is occupied elsewhere or exhausted from his defense efforts. A third class of males

may wander through the entire area, avoiding other males but searching for females. Particular strategies may have energetic or age-specific advantages (Constantz, 1975).

Countering these male strategies, females will make varying degrees of choice depending upon the number of males available. How females recognize the fitness of a courting male remains problematical (Ehrman, 1972). Darwin (1871) first stated that females may select males for their phenotypic appearances without regard for the actual adaptiveness of these features. Later investigators have shown some characters, which Darwin attributed to females choice, actually have adaptive value in male-male competition for females (Selander, 1972). In other cases, territory quality may be so important for the female that she will pick an area for its physical qualities rather than the male present upon it (Verner, 1964; Orians, 1969). Females may use some combination of the male's genetic fitness and his area in choosing a mate.

In order to understand how behavior or other attributes of males contribute to their fitness, it is important to demonstrate how phenotypes correlate with individual RS. Trivers (1972) reviewed a number of characters that have been identified as important to male RS. Since male RS will be measured in this study, I will attempt to identify those attributes of male S. jarrovi which correlate with their RS.

Larger body size or greater age, as indicators of the male's ability to survive, have been implicated as

important to RS 1) directly, 2) through the assumed correlation between size and dominance rank and 3) in studies of sexual dimorphism where males are larger than females. Trivers (1972) found larger male Anolis grahami copulated more frequently than small males. Dominant males in other species are more successful (Scott, 1942; DeVore, 1965; Harris, 1964; LeBouef and Peterson, 1969). In the boat-tailed grackle (Selander, 1965), larger size is favored in males for mating success even though higher mortality accompanies larger size.

Aggressive behavior is among the parameters which are assumed to correlate with RS but are more difficult to measure. Assessment is hindered by site-dependent aggressiveness and by variance in the quality of the area defended. Usually aggression is measured indirectly through territory size. Only a loose correlation between breeding success and territory size may be expected, however, unless territories are rather uniform in desirability. The diversity of territorial patterns, even with particular taxa, has hindered understanding of the underlying mechanisms (Noble, 1939; Carpenter, 1958; Brown, 1964). Brown and Orians (1970), in reviewing the subject, emphasized the need for demonstrations that animals acting in one way, such as possessing exclusive territories, had higher RS than animals acting in some other way. It is necessary to show the result (RS) the animal gets for its defense efforts.

The degree to which territorial behavior can vary is well documented among lizards. Species may be non-aggressive (Barwick, 1959), highly aggressive but non-territorial (Carpenter, 1962; Christiansen, 1971), moderately territorial (Fitch, 1940; Carpenter, 1967; Rand, 1967; Ferner, 1974) or highly territorial (Tinkle, 1967; Milstead, 1970). Among territorial species variation in aggressive levels has only recently been related to ecological factors. The intensity of aggressive defense may vary within a species (Tinkle, 1967) and between closely related species with distinct demographic characteristics (Vinegar, 1975a). The amount of variation in aggression levels within one population has not been quantified. A common pattern of defense in several species is a well defended core area with less vigorous defense at marginal areas (Harris, 1964; Yedlin and Ferguson, 1971). One measure of defense is the amount of overlap between territories which may be low (Tinkle, 1967) or vary seasonally (Ferner, 1974).

Elucidating the adaptiveness of aggression and territoriality in a lizard requires identifying the means by which territory holders achieve RS. Seasonal variation in spatial patterns may be suggestive; that is, comparisons between breeding and non-breeding periods might illustrate how the immediate RS gain during the breeding season alters the selective value of aggression. The species chosen for study, Sceloporus jarrovi, has a fall breeding season (Goldberg, 1971). Because this contrasts with the common

lizard pattern of spring or early summer breeding, S. jarrovi is potentially useful for comparisons of behavioral patterns between species. It should be possible to correlate fall breeding with behavioral strategies not found in spring breeding lizards.

Because hierarchical social systems in lizard populations may occur in locations where food is localized (Evans, 1951), vegetation obscures individuals (Stamps, 1973), or delayed breeding may be advantageous (Berry, 1074), lizards may be ideal subjects for investigations into the selective contexts of different social systems. Davis (1958), Willis (1967), and Hunsaker and Burrage (1969) suggested that dominance hierarchies and territories might be best viewed as opposite ends of a behavioral continuum rather than as discrete entities. Hunsaker and Burrage (1969) suggested that the critical factor in the behavioral switch among lizards was density. They viewed hierarchical systems as adaptive plasticity in the behavior of individuals that enabled them to exploit concentrated food sources. However, the observation that components of both territorial and hierarchical structures may occur simultaneously within one population (Stamps, 1973; Berry, 1974) suggests that factors other than density may be important. Density is probably correlated with factors such as food levels or survivorship, which are the real selective contexts for hierarchical behavior.

If hierarchical behavior is adaptive, and the territory-hierarchy continuum is an appropriate model, elements of

hierarchical behavior should occur in populations which do not exhibit classical hierarchies. The adaptive value of dominance is generally obvious, although some reports of beta males breeding more successfully than alpha males have appeared for mammals (Jolly, 1966; Rabb, Wolpy, and Ginsburg, 1967). However, the selective pressures favoring submissive behavior have not been measured in field populations. The probability of successful breeding in subsequent years by subordinates should be a primary consideration in the evolutionary maintenance of submissive behavior. If subordinates have a high probability of breeding later, submissive behavior would be adaptive when current situations prevent breeding. If the probability of breeding later is low, subordinate behavior should not persist in the population, unless there are other factors promoting its maintenance. Migration or escalated fighting for females may be a better strategy for subordinate animals under these circumstances. This potential for hierarchical relationships in a lizard was explored in S. jarrovi as an alternative reproductive strategy to territoriality.

Coupled with the array of social structures in lizards indicated above are a wide variety of life cycle patterns. Some species are oviparous while others are ovoviviparous (ecologically viviparous). Demographic characters of populations may vary within species (Pianka, 1967; Tinkle, 1967; Tinkle and Ballinger, 1972) and between species (Tinkle,1969b; Tinkle, Wilbur and Tilley, 1970; Fitch, 1970;

Licht and Gorman, 1970). Tinkle, Wilbur and Tilley (1970) recognized two basic life history patterns: 1) early maturing species with multiple clutches and 2) delayed maturing species with single clutches. The discovery of intraspecific variation (Tinkle and Ballinger, 1972) and some unexpected combinations of characters in other species (Tinkle, 1973; Ballinger, 1973) indicate the need for revision and extension of current theory. Local variation in demographic characters is now recognized in several lizards (Blair, 1960; Vinegar, 1975b; Van Devender, 1975).

The conditions which favor the evolution of viviparity in reptiles are unknown (Neill, 1964; Fitch, 1970). In reptiles viviparity is associated with delayed maturity (Tinkle, Wilbur and Tilley, 1970; but see Ballinger, 1973). Like other reproductive strategies which delay the age of maturity, viviparity seems to reduce the organism's reproductive potential and should not be favored (Cole, 1954; Lewontin, 1965). Explanations for the evolution of strategies with delayed maturity have generally emphasized low or unpredictable prereproductive survival (Murphy, 1968; Hairston, Tinkle and Wilbur, 1970; Gadgil and Bossert, 1970; Goodman, 1974; Bell, 1976). Since viviparity has arisen independently in a number of unrelated phylogenetic lines among the Reptilia, the conditions favoring viviparity must occur rather frequently.

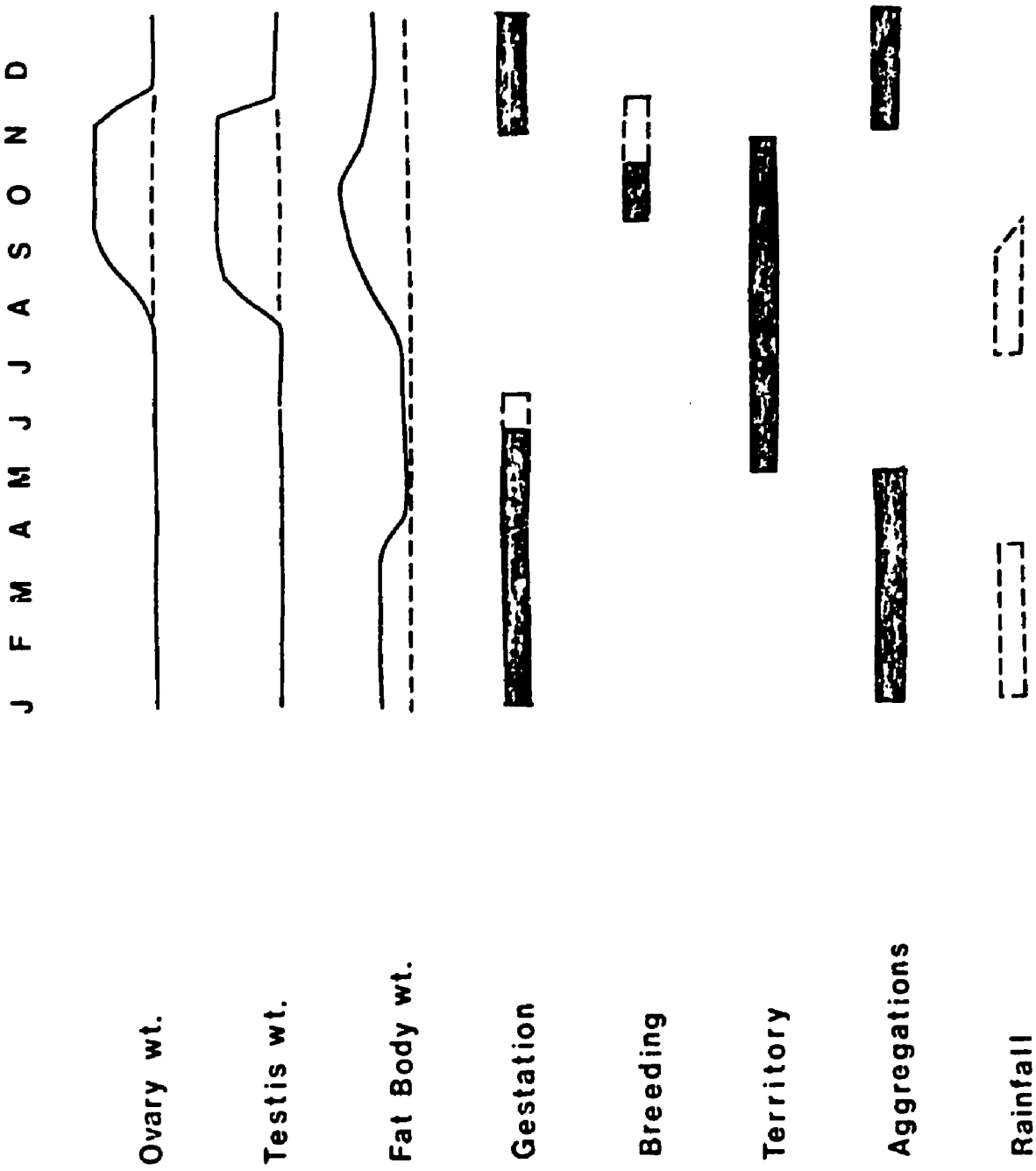
A number of advantages and disadvantages of viviparity in reptiles have been identified (Fitch, 1970). The

potential demographic disadvantages include delayed maturity and reduced annual egg production. Gravid females potentially suffer from high predator pressures. They are burdened by their litters and capture by a predator means the simultaneous loss of the litter. However, viviparous reptiles have eliminated nesting losses and can control the developmental rate of the embryos through behavioral means. The latter advantage may explain why the proportion of viviparous species in the reptile community increases with altitude (Weeks, 1935), where nesting sites are more restricted.

The demography and behavior of only a few viviparous lizards is known in any detail (Ballinger, 1973; Vitt,1973). The viviparous lizard Sceloporus jarrovi was chosen for my study because it is 1) diurnal, 2) abundant, and 3) relatively insensitive to the presence of observers. Some aspects of the life history (Goldberg, 1971; Ballinger,1973; Simon, 1975) have been studied in Arizona populations (see Figure 1). As mentioned previously, the species has a fall breeding season. The young are born in the spring after a gestation of about seven months. One result of this cycle is that about half of the age cohort attain sexual maturity at six months of age (Ballinger, 1973). This early maturation equals or precedes that of most oviparous forms. The species is montane in distribution but remains active year-round (Burns, 1970). Basking during the winter apparently speeds the development of embryos within gravid

Figure 1. The annual cycle of Sceloporus jarrovi. Information is gathered from several sources including this study.

Figure 1


J F M A M J J A S O N D
Ovary wt.
Testis wt.
Fat Body wt.
Gestation
Breeding
Territory
Aggregations
Rainfall

females (Tinkle and Hadley, 1973). The function of winter basking by males is unknown. This array of unusual life history patterns suggests this species may be useful in identifying advantages of viviparity. The proposed advantages of winter basking may be very important in contributing to the success of the observed life cycle.

The behavioral ecology of S. jarrovi was investigated with emphasis on three questions: 1) What is the adaptive value of aggressive and territorial behavior in this species? 2) What phenotypic attributes of males correlate with their reproductive success? and 3) How does winter basking contribute to a viviparous reproductive strategy?

THE STUDY SITES AND GENERAL METHODS

The mountains of southeast Arizona, including the Pinaleño Mountains where the study was conducted, form islands of moist habitats surrounded by low elevation desert and grassland. Elements of the Sierra Madre Occidental fauna and flora combine with Rocky Mountain species to make the region particularly rich in species diversity, especially of insects. The area has sharply seasonal rainfall, coming during the winter months from the west and during July and August in thunderstorms from the southeast. Lowe (1964) presents general information about the region. Rainfall and temperature records for the duration of this study were obtained at Safford, Arizona (elevation 885 m), the weather station closest to the study area, and are shown in Appendix I. For the purposes of this study, Spring (May-June) was a period of little precipitation and rising temperatures. Summer (July-August) experienced the greatest monthly precipitation, and temperatures were modulated from June peaks. Fall (September-October) had less rainfall than the summer and cooler temperatures.

The study population of Sceloporus jarrovi was located at about 1825 m in the Pinaleño Mountains near Safford, Arizona, close to the northern end of the species range. Field observations were made May 10-November 15, 1972 and May 1-December 10, 1973 and 1974. The study area for the bulk of the observations ("summer site") was a small rocky

canyon in a pine-juniper association. An ephemeral stream flowed through the midline of the study area during wet months. Boulders and large flat areas of rock were scattered through the canyon. Approximately 0.60 hectare was measured and surveyed in 1972. This was expanded to 0.75 hectare in subsequent years in order to include some animals overlapping one boundary of the original study area. In order to keep data consistent, density estimates throughout this study were based upon the original boundaries. The study area was measured off in 7.6 m (25') intervals and a map of landmarks made. In the summer site, 293 animals were recaptured 491 times.

A second site ("winter site") was a long rock-cut near the summer site where the animals aggregated in November (see Chapter IV). This site was approximately 150 m long and the rock cliffs varied in height from five to 15 meters. Animals in this area were studied in early November 1972 and November 1-December 10, 1973 and 1974. At this site, 259 animals were marked.

All animals in the summer site and most in the winter site were captured, toe-clipped, marked with paint and released (as in Tinkle, 1967). Upon capture, snout-vent and tail lengths (whole or regenerated) were measured to the nearest millimeter and ventral body color was noted. Animals were recaptured only after molting, which removed the paint marks. Study area margins were searched at irregular intervals to assess migration.

Adults were animals that had overwintered at least once, regardless of whether they were sexually mature in the previous fall (Ballinger, 1973). Animals born in the current year were called young (26-54 mm SVL) or yearlings (> 54 mm). In this study, all yearlings will be assumed sexually mature. Published data (Goldberg, 1971; Tinkle and Hadley, 1973) strongly suggested 54 mm SVL distinguished sexually mature and immature individuals in the fall. Observations in the Pinalenos during this study supported this estimate of size at maturity. Males acquired their deep blue throat color at this size during the fall (see Chapter III). Palpation of females smaller than 54 mm failed to indicate the presence of enlarged eggs or embryos in the fall.

Procedures and manipulations for answering specific aspects of the three questions explored are given in each chapter. In addition, a primary goal was observing as much undisturbed behavior of animals as possible. Nearly 1400 manhours were spent in the study sites. Additional time in the field was spent collecting animals for various purposes and setting up insect traps (see Chapter II). Most animals were not disturbed by the presence of an observer. The use of 7x binoculars enabled close-up observations at distances from 5 to 20 meters. Behaviors of individuals apparently disturbed by the presence or movement of the observer were discarded. Some behaviors were filmed using a Bolex 16mm movie camera.

CHAPTER II

SEASONAL CHANGES IN TERRITORIAL BEHAVIOR

Territoriality, generally defined as the defense of an area against conspecifics (Noble, 1939) is a common spacing device in vertebrates. The important evolutionary question about territoriality is what factors select for individual aggressiveness with respect to space (Brown and Orians, 1970). It is necessary to show that territorial individuals have greater RS than individuals behaving in other ways. For example, high levels of aggression only during the breeding season would indicate that aggression contributes to RS. I conducted a three-year study of the territorial system of Sceloporus jarrovi to determine its adaptive value, particularly in the context of a fall breeding season.

Territoriality is a common phenomenon among iguanid lizards but its adaptive value has been clearly demonstrated in only a few species (Rand, 1967; Tinkle, 1969). Many studies on home ranges and territories in lizards ignore seasonal effects by obtaining capture locations over prolonged periods, fail to quantify aggression data (but see Vinegar, 1975a), and provide superficial information about breeding structures. With the exception of Ferner (1974), seasonal data on aggression or territory sizes in lizards have not been quantified.

Factors which select for specific levels of aggression in lizards are still unknown. Different aggression levels

have been correlated with demographic characters of the population (Tinkle, 1967; Vinegar, 1975a), food levels (Evans, 1951) or topography (Stamps, 1973; Brattstrom, 1974). In dense populations presumably supported by high food levels, territoriality may break down into a hierarchical social structure (Evans, 1951; Hunsaker and Burrage, 1969; Stamps, 1973; Berry, 1974).

Levels of aggression may be compared between species, or within a species on a seasonal basis, by examining the display repertoire (Carpenter, 1967), the frequency of encounters between conspecifics (Vinegar, 1975a) or spatial patterns of defense (Harris, 1964; Yedlin and Ferguson, 1971). The effectiveness of territorial defense may be measured indirectly through the extent of territorial overlap (Tinkle, 1967; Ferner, 1974).

As part of a long-term study on the behavior of the lizard S. jarrovi, I explored the adaptive nature of aggressive behavior with respect to space by addressing the following specific questions: (1) Do seasonal changes in aggression and territory size occur? (2) When are territories established and what factors influence the choice of location? (3) What is the relationship between territory size and estimates of activity? (4) How does density affect aggression and territory size? and (5) Do sexual differences exist in aggression and territoriality?

METHODS

Daily locations of marked animals in the summer site were recorded, as were encounters between animals which I observed, from May through October. I attempted to locate all active lizards during each visit to the site. The context of various displays were determined from the natural encounters observed. Aggression levels, territory size and overlap, and activity were quantified on a monthly basis to determine whether there were seasonal changes.

Aggression was measured through natural and staged encounters. Encounters were classified into four "types."

I. Foreign male introduced to resident male

II. Foreign female introduced to resident male

III. Foreign male introduced to resident female

IV. Foreign female introduced to resident female

In some natural encounters, the residency was designated arbitrarily. The frequency of natural encounters was calculated per manhour on a daily basis and averaged over a month. Twenty encounters of each type were run between tethered animals and unrestricted adult residents each month between May and October 1972 and 1973 to assure sufficient controlled observations. Some additional male-male encounters were run in May and June 1974. Tethered animals were captured outside the study area and utilized for one or two days. These animals, when introduced within several meters of a resident, were tied by a long fish line to a bamboo pole and given generous slack in the line to allow

them free movement. No attempt was made to match sizes of tethered and resident animals, and a particular resident was tested no more than three times in a month with a given sex of tethered animal.

Encounters were ranked according to the level of aggression of the resident. I used the following behaviors, listed in roughly ascending level of excitement, as indicators of level of aggression during observed interactions:

1. Bobs: head-nods which most frequently occur as the first sign of recognition of a conspecific but may occur after moving or eating.
2. Pushups: flexion and extension of the forearms to raise and lower the anterior body in a pattern similar to that described for head-nods above (Carpenter, 1962). This is a more intense version of the bob pattern and occurs early in an encounter.
3. "Fullshow": a simultaneous display of arched back, flattened sides, gular show and extended legs. While in this posture, the animal may perform pushups with the intensity of the display declining as the pushups continue. Components of this behavior may occur separately or in various components, providing a graded response. The vigor of the display (extent of arch and side-flattening) varies with the intensity of the moment. This display, which serves to make the individual appear as large as possible, generally

occurs when an intruder fails to move away after a pushup display.

4. Shudder-bobs: rapid up and down nods of the head given while stationary or approaching another animal. This display is given most frequently in courtship by males toward females, but it also occurs in aggressive contexts involving either sex (Ruby, 1977).
5. Faceoff: an exaggerated fullshow display while laterally oriented toward an intruder, each animal facing in the opposite direction (Carpenter, 1963). Individuals may gape with their mouths and attempt to bite the tail of the other animal. Circling and bluffing attacks occur frequently. In addition, one or both animals may do side-swaying motions with tail lashing. The lashing does not strike the opponent in any apparently deliberate way.
6. Charge or attack: a head-first dash at an intruder who has not withdrawn. The intruder may respond with a faceoff display, a submissive display (pressing of the body against the substrate) or retreat. Charges are also elicited by a sudden retreat of the intruder. Charging animals may emit a guttural hissing sound at their target. This was the only sound observed.

I ranked encounters by level of aggressiveness as follows:

level 0 no response or resident ignores intruder

level 1 bobs or pushup display

level 2 "fullshow"

level 3 shudder-bobs

level 4 charge, attack or faceoff

The intensity of natural encounters was compared on a seasonal basis to identify shifts in level and to establish whether a negative correlation existed between the frequency and intensity of natural encounters. Results of staged encounters were compared (1) between months for each sex, (2) between the sexes for the same month, and (3) between years for the same months.

I determined the effect of body size upon aggression levels and frequency of winning in both natural and staged encounters. Animals in all intrasexual natural encounters were identified as "winners" or "losers" based on (1) intensity of display by each combatant and (2) the retreat or submission of one animal. The aggression scores for the winning lizards involved in these encounters were sorted into five categories based on size (SVL) differences between the combatants, and tested for differences between size groups. Since mean body size increased during the year and may directly affect aggression levels, I compared the scores of tethered encounters in two age classes (second year and older animals) for each month. Because the variance in tethered encounter scores was widest among males in the spring (May-June), all male-male encounters during that period were sorted according to three age classes of

residents and two sizes of introduced animals and tested for differences in aggression levels. All analyses of ranked scores were done with nonparametric tests (Mann-Whitney U Test; Siegel, 1956).

Potential exclusion of small males by larger males from the study area was investigated by testing sex ratios of each age class for deviation from a 1:1 ratio using a Chi-square test. Sex ratios were calculated from weekly censuses. Individuals seen at least once in a week were counted for that week. Those animals not seen in a given week but observed during both the preceding and following weeks were also included in that week's total.

Territories were defined as the area encompassing all sightings during a month for a given individual. Although this total area is usually called a home range, I called it the territory because of evidence that all or nearly all of it is defended by adults. Sightings of individuals were mapped and the outermost points connected to form a polygon. The area of the polygon was determined and then converted into an estimate unbiased by sample size using the method of Jennrich and Turner (1969). Mean territory size was determined monthly and tested for sexual, seasonal and annual changes. Sizes of territories held by the same individual were compared between months of the same year by pairwise tests to determine if changes in sample means were reflected in territory sizes of specific individuals. The degree of territorial overlap was defined as the percentage of the territory (the polygon above) that was shared with all

other adult lizards of the same sex. I attempted to correlate broad territorial overlap with observed dominance/subordinance behavior. Territory sizes and overlaps of yearlings were computed separately from adults and similarly tested for sexual and seasonal changes.

To measure fidelity to territory site, the geometric centers of activity for May and for the breeding season (September 15 to October 15) were computed for all resident adults common to both periods. The difference between the two centers, the distance moved, was determined by trigonometry and tested for sexual and annual differences. The shift distance was also tested for correlation with spring and fall territory sizes.

Since my data indicated females were more sedentary than males, during 1974 I investigated five factors that might influence selection of the spring territory site of females: 1) percent rocky substrate, 2) number of crevices suitable for a lizard, 3) food abundance, 4) presence of either sex, and 5) previous use of the area. A circular area around each of 30 evenly spaced sites, with a radius equal to one half of the mean distance between sites, was identified. The 30 locations were arranged as five transects of six sites each (Appendix II). The percent rock cover per area and the number of crevices large enough for a lizard to enter were estimated for each of the 30 areas. To measure food availability, a $10cm^2$ masonite board covered with "Stickem Special" was placed in the center of each area for a 24 hour period (=trial) on June 2 and 22, July 10

and 30, August 19 and September 24, 1974. Food abundance was determined by counting all insects, regardless of size, collected on the sticky traps. Food values at a particular site were examined for correlations between values for different trials and with the average food values for the six trials. Food values of the outer two locations on each transect were tested against values of the inner two locations of the transects for each trial. The degree of rockiness, number of crevices and food measures for each of the six trials were compared with density estimates for each date. Densities were the number of animals seen within each circular area during a span of five days centering on the date of the trial.

Possible behavioral factors in choosing a territory were considered by examining female territories in May for overlap with territories of 1) males in May, 2) other females in May and 3) the same female during the previous October, if known. Territories were arbitrarily considered to have overlapped when two or more sightings for an animal were within the territory of another animal.

Activity patterns, which might affect estimates of territory sizes, were measured in two ways. "Daily frequency" was defined as the number of days a resident was sighted during a month expressed as a percentage of the number of visits per month. "Distance moved" in meters/hour was determined by watching particular individuals for at least one hour hour at a time. The average distance moved per hour was computed for the months May through October for

both 1973 and 1974. The same individual was rarely watched for an entire day but several hours of continuous observation were possible.

Because aggression levels seem correlated with density in lizards (Tinkle, 1967; Brattstrom, 1974; Vinegar, 1975a), densities of lizards in the summer site were monitored. Counts of adults and young seen within the original boundaries of the study area (0.60 ha) were made on a monthly basis. Densities were the number of individuals seen at least three days during a month, and thereby considered residents.

Aggression, territoriality, and activity were separately tested for changes between months and over a period of several months by appropriate statistical tests (Remington and Schork, 1970; Siegel, 1956). Means were reported with their associated standard errors, unless otherwise indicated. Ranked aggression scores were tested by non-parametric tests, as no assumption of normality was made for these data. Where statistically significant changes occurred (for example, in territory size), I examined other characters (aggression, activity, etc.) for parallel effects to determine the interaction, if any, between observed behavioral patterns.

RESULTS

Aggression

A primary goal of this study was to assess the adaptive value of aggressive behavior in S. jarrovi. Seasonal, spatial or sexual variations in level of aggression could identify the resource(s) being defended. Correlation of high aggression levels among males with the breeding season, for example, would suggest that females were the resource being defended. Sexual differences in level or pattern of aggression would indicate that the sexes were responsive to different resources. I sought to answer three specific questions related to aggressive behavior: (1) Do seasonal changes in aggression occur? (2) What sexual differences in level and pattern of aggression exist? and (3) How does body size affect the outcome of aggressive interactions?

Both sexes were aggressive to their own and the opposite sex. The frequency of natural encounters between animals is shown in Table 1. Most natural encounters occurred between neighbors; the previous history of interaction between them might have influenced the displays observed. Natural encounters of male residents with either sex increase in frequency from May to October (ANOVA, $p<.01$). This increase in encounter frequency is associated with less tolerance between males (see below) and greater activity of males (see Figure 16). Displays at neighbors over long distances (up to 20m) were observed only during the breeding season of each year. Encounters in which males displayed at females

TABLE 1

MEANS AND STANDARD ERRORS OF THE FREQUENCY OF OBSERVED ENCOUNTERS BY MONTH PER MANHOUR EFFORT 1972-74. PARENTHETIC VALUES ARE THE ACTUAL NUMBER OF ENCOUNTERS

Month	Encounter Type			
	Resident Male Foreign Male	Resident Male Displayed at Female	Resident Female Displayed at Male	Resident Female Foreign Female
	N= 69 (X 100)	N=378 (X 100)	N= 21 (X 100)	N= 79 (X 100)
May	2.02±2.96 (4)	12.71±5.29 (22)	0.75±2.15 (2)	6.93±4.16 (13)
June	3.02±3.57 (6)	12.31±5.73 (24)	4.66±3.94 (7)	9.00±5.42 (18)
July	2.89±3.27 (6)	21.80±6.16 (35)	3.38±3.95 (5)	9.76±4.93 (16)
August	4.89±4.01 (9)	21.14±5.57 (38)	1.25±2.54 (3)	6.96±4.43 (12)
September	10.45±4.63 (19)	58.54±7.38 (150)	0.71±2.10 (2)	4.07±3.61 (14)
October	18.29±5.59 (25)	64.83±7.49 (109)	0.63±1.85 (2)	6.74±4.40 (6)
Average	6.56±4.32	30.6±6.76	1.92±3.15	7.24±4.59

increase significantly (ANOVA, $p<.05$) as the fall breeding season approaches and males search for females. Female residents did not show any significant change in frequency of encounter with other females during the year, nor in frequency of encounters in which they display at males.

Intensity of display in male-male encounters increased to a peak in the fall months (Kruskal-Wallis test, $p<.05$), paralleling the increase in frequency of such encounters. On the other hand, female-female intensity of aggression was highest during the summer (Kruskal-Wallis test, $p<.05$). This suggests that intensity and frequency of encounters are not correlated in females.

The staged encounters provided a baseline for comparing the aggression levels in natural encounters. Results of these experiments are shown in Figures 2 and 3. Several seasonal patterns of aggression were identified in S. jarrovi. Intensely aggressive responses in male-male encounters increased in frequency steadily from May to October (Mann-Whitney U test, $p<.05$). The wide variance in male-male aggression observed in the spring was greatly diminished in the fall. This increasing level of aggression correlated with the trends observed in natural encounters. Resident males showed a high attack (level 4) tendency toward females in the spring. During July, males switched to a high shudder-bob frequency toward females ($p<.05$). In the fall, these shuddering displays were associated with courtship.

The level of female-female aggression was consistently bimodal in distribution (Figure 3) with a significant change

Figure 2. Ranked aggressive responses by male resident Sceloporus jarrovi to introduced conspecifics. Each histogram represents scores from 36 to 48 (mean= 42.0) staged encounters. Diagonal hatching represents encounters which resulted in copulations.

Figure 2

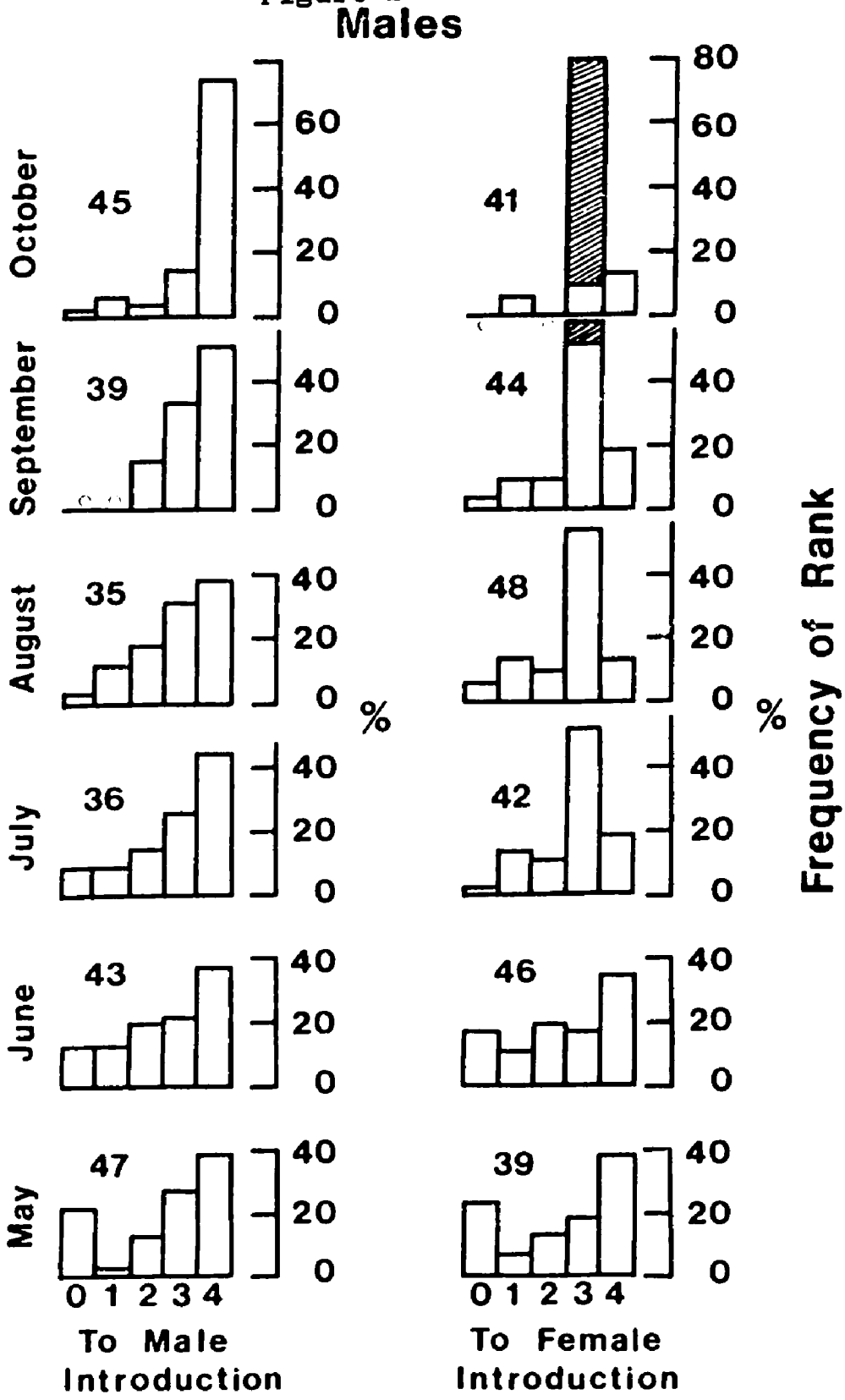
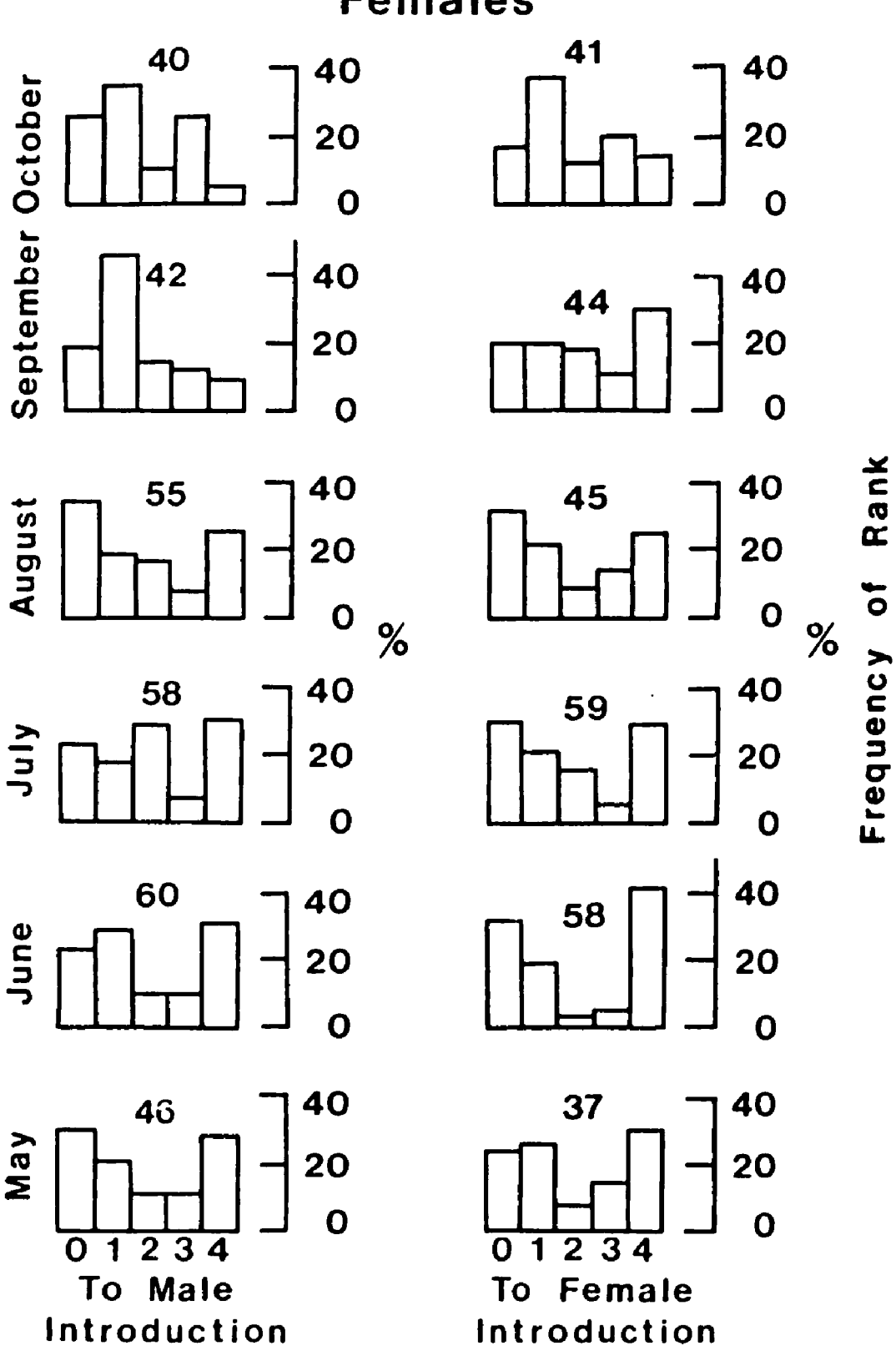

Males
October
September
August
July
June
May
45
41
39
44
35
48
36
42
43
46
47
39
80
60
40
20
0
%
Frequency of Rank
0 1 2 3 4
To Male Introduction
To Female Introduction
Ranked Response

Figure 3. Ranked aggressive responses by female resident *Sceloporus jarrovi* to introduced conspecifics. Each histogram represents scores from 37 to 60 (mean= 49.5) staged encounters.

Figure 3


Females
September October
August
July
June
May
40
41
42
44
55
45
58
59
60
58
46
37
40
20
0
%
Frequency of Rank
0 1 2 3 4
To Male Introduction
To Female Introduction
Ranked Response

to lower levels of aggression from September to October ($p<.05$). Female aggression toward introduced males tended to be highest in the spring and lowest in the fall. However, during four months (May, July, August, September), females were more aggressive toward males in 1973 than in 1972 (Mann-Whitney U test, $p<.05$). This was the only difference between years found in any of the encounter types. The reason for this difference between years is unknown.

The staged encounters provided only limited insight into the pattern of defense within an animal's territory, because each animal was tested only two or three times per month with other lizards of the same sex. It was not possible to demonstrate variation in levels of aggression exhibited in different regions of the territory. However, most animals responded to the intruder regardless of their location within their territory. Hence I believe that considering the entire home range as a "territory" is appropriate. Changes in the minimum distance which provoked responses were apparent during the year. Tethered animals placed more than three meters from a resident male were more likely to provoke responses in late summer and during the fall than in earlier months. Only a few female residents would react to intruders at distances greater than two meters. Pursuit of a retreating intruder by residents of either sex during the spring or summer was generally short, up to five meters. During the fall breeding season, males were observed to pursue other males up to 15 meters.

Body size is usually a good predictor of which combatant will "win" an encounter (Figures 4 and 5). The larger of the two animals (119 of 150, $\chi^2=64.03$, $p<.01$) generally won the encounter (Table 2). The proportion of encounters lost by larger animals was not significantly different ($\chi^2=3.13$, NS) between the sexes. Among the twenty-three encounters in which the smaller animal won, ten (43%) involved differences in SVL between combatants of five millimeters or less.

When aggression scores of these natural encounters (N=150) are tested according to the SVL difference between combatants, I determined that the frequency of charges or attacks (level 4) in male-male natural encounters increased as the size differences increased (Mann-Whitney U test, $p<.05$). Encounters between males of great disparity in size were shorter and less complex (fewer display sequences). Apparently the larger male can attack without risk of counterattack when the size difference between animals is greater. A similar test on the female-female encounters proved not significant, but the data suggested that the trend was toward lower aggression as the size difference of combatants increased, in contrast to the male pattern.

Some of the increase in male aggression during the year can be attributed to SVL increases during their second growing season. Whereas adult body sizes range nearly 35mm (60-94mm) in the spring, by fall the range has been reduced to about 20mm (75-94mm). Male-male staged encounters show increases in aggression level during the year for both

Figure 4. The relationship between body size and the outcome of intrasexual aggressive encounters in males. N=73. The diagonal line represents equal sized combatants.

Figure 4

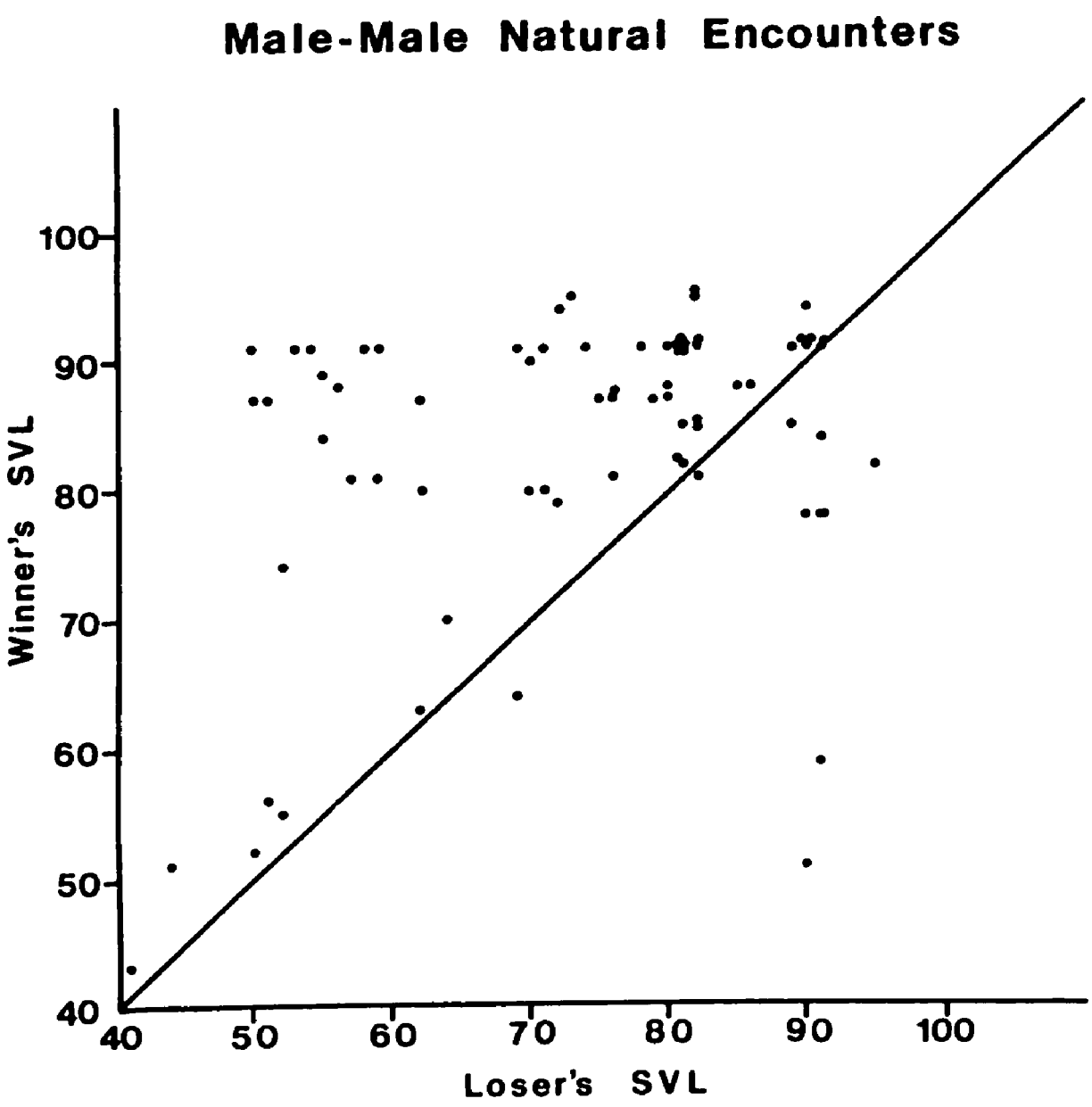

Male-Male Natural Encounters
Winner's SVL
Loser's SVL
40
50
60
70
80
90
100

Figure 5. The relationship between body size and the outcome of intrasexual aggressive encounters in females. N=77. The diagonal line represents equal sized combatants.

Figure 5

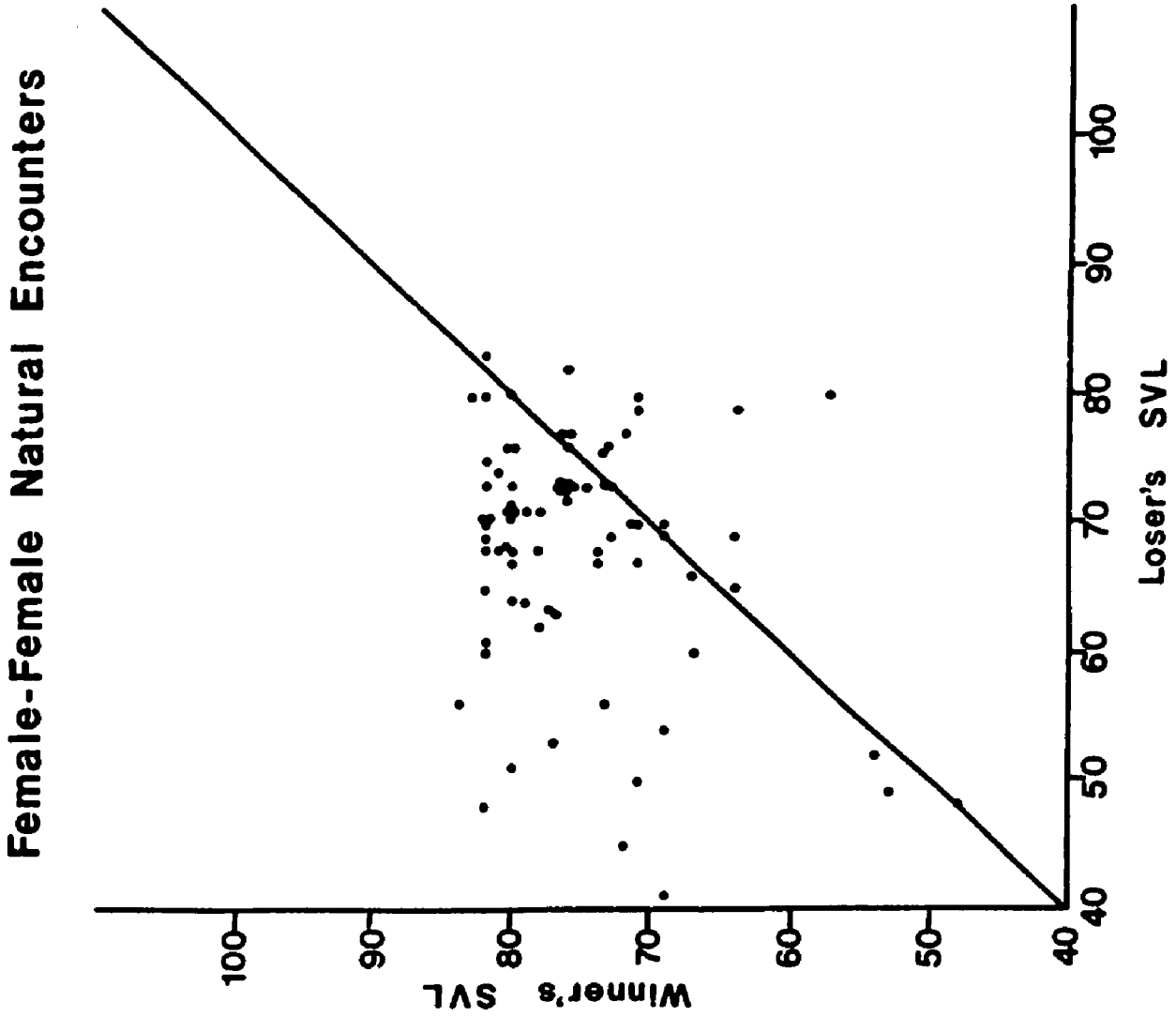

Female-Female Natural Encounters
Winner's SVL
Loser's SVL
40
50
60
70
80
90
100

TABLE 2

THE EFFECT OF BODY SIZE UPON FREQUENCY OF WINNING IN INTRASEXUAL ENCOUNTERS.

	Winning Animal			
	Larger	Equal	Smaller	Total
Males	61	2	10	73
Females	58	5	14	77
Total	119	7	24	150

age classes (second year and older) with no significant differences between groups for a given month. However, residents of the two age classes can be distinguished by their reaction to second-year intruders (60-70mm) during the spring months. The older males, much larger than the intruders, showed significantly higher (Mann-Whitney U test, $p<.05$) levels of aggression than did the second year residents (Table 3). The significance seems to result from the more numerous zero responses by second year residents rather than more numerous maximal responses by older residents. The response to other sizes of introduced animals did not vary with the size of the resident. The difference in response to a second year intruder suggests that the wider variance in spring aggression levels (Figure 2) correlates with the greater range of body size at that time.

One result of larger animals winning encounters should be competitive exclusion of smaller animals from the study area. Evidence other than encounter outcomes which supports a hypothesis of competitive exclusion of smaller males comes from examination of sex ratios of different age classes. Examination of near-term litters indicated the primary sex ratio was close to 1:1, as expected at the termination of parental care after birth (Fisher, 1958). However, an unbalanced sex ratio favoring females developed among second year animals in 1972 and 1974 but not in 1973. This skewness reached significant levels (χ^2 test, $p<.05$) for extended periods during these two years (see Figure 6). Neither the

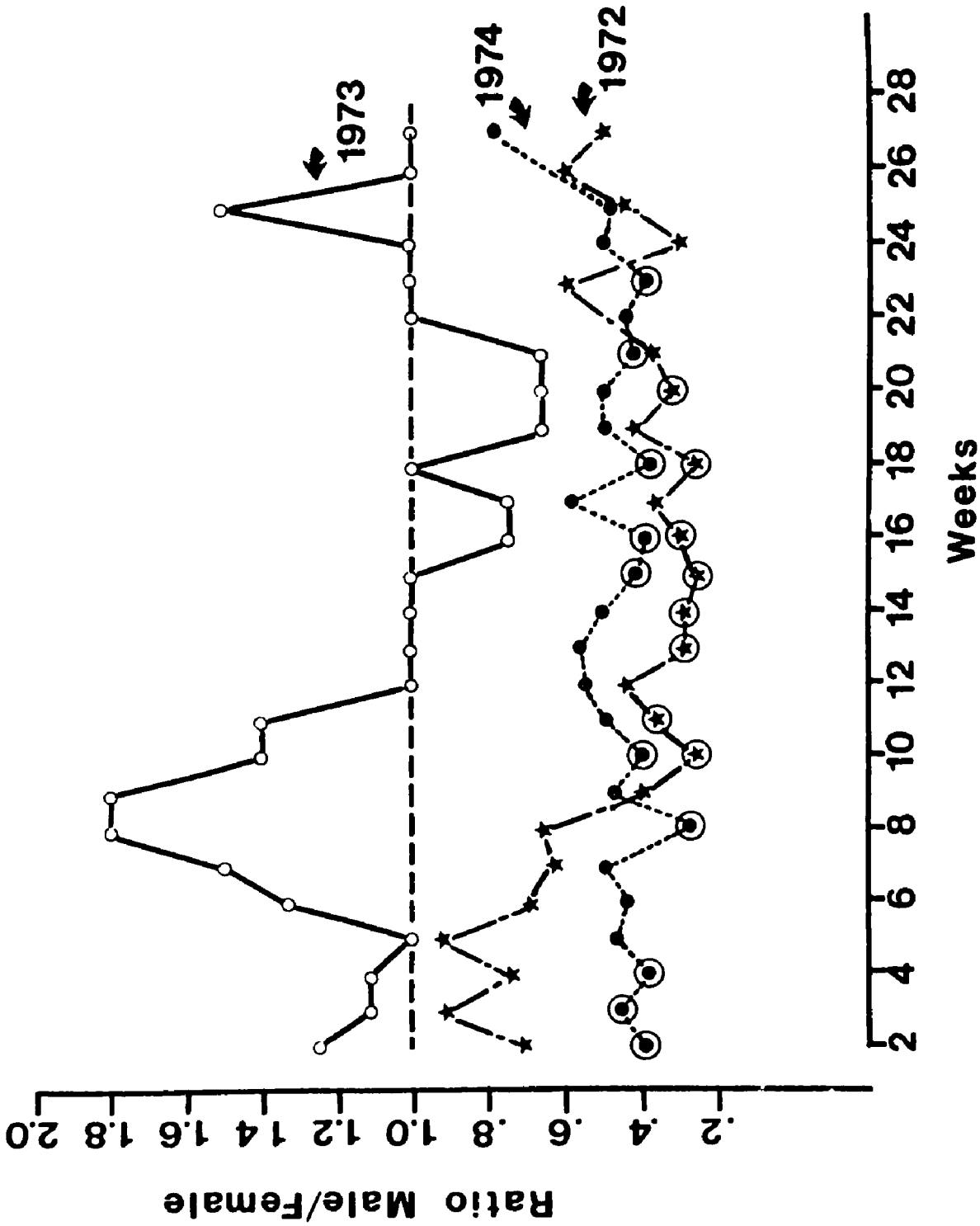
TABLE 3

MALE RESPONSES TO INTRODUCED MALES BY RANKED LEVELS OF EXCITEMENT FOR ALL STAGED ENCOUNTERS IN MAY AND JUNE, 1972-74.

Size of Resident	Size of Introduced Animal				
	60-70mm		80-90mm		
	Score	N	Score	N	Sig.
60-69mm	0	5	0	2	
	1	1	1	3	
	2	4	2	4	.04
	3	6	3	4	
	4	5	4	6	
	N =	21	N =	19	
70-79mm	0	0	0	3	
	1	0	1	1	
	2	1	2	1	NS
	3	1	3	2	
	4	2	4	1	
	N =	4	N =	8	
80+	0	1	0	3	
	1	2	1	6	
	2	1	2	3	NS
	3	2	3	3	
	4	11	4	14	
	N =	17	N =	29	

Figure 6. Sex ratios (male/female) of second-year resident animals in the study area for each year. Circled points represent significant ($p < .05$) deviations from the predicted 1:1 ratio using the chi-square test.

Figure 6


1973
1974
1972
Ratio Male/Female
2.0
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Weeks

young or older age classes showed more than two isolated weeks in any year when the ratio was significantly skewed. Sensitive testing is not possible among the oldest age class due to small sample sizes. The effect of exclusion is most clearly seen in 1972, when sex ratios in May are close to unity, but rapidly become skewed during June. An alternative hypothesis would be that the skewness results from differential predation upon males. Males are not more conspicuous during June, so I doubt they would encounter predators more frequently than females. Sample sizes of the older age class are too small to determine whether the skewness persists.

In general, seasonal changes in aggression levels were demonstrated. Male-male aggression increased in frequency and intensity as the fall breeding season approached. Female-female aggression varied in intensity but not frequency during the year. The area used by an animal during a month is generally defended throughout and can be considered a "territory." Encounter outcomes are strongly influenced by the relative sizes of the combatants. Larger animals win most encounters. Among males, encounters with the most intense display are between animals of great disparity in size. Males closely matched in size will avoid attacks and use faceoff displays. The most intense encounters between females are apparently between similarly sized individuals. As a result of larger animals winning most encounters, smaller males are often excluded from the study area by larger males. Data on food levels (Figure 12)

indicated the value of locations within the study area as opposed to the surrounding area.

Territoriality

Territoriality develops when defense of an area containing critical resources is economical (Brown, 1964; Brown and Orians, 1970). Defendable resources may include mates, nesting sites, display perches, roosting places or food. The parameters of territories generally considered important are its size, resources and position relative to others. Some controversy over estimates of size exists (Tinkle and Woodward, 1967; Jennrich and Turner, 1969; Milstead, 1971, 1972; Turner, 1971) because of sample size effects. Resources are more difficult to quantify because animals selectively utilize their habitat and observer recognition of the critical resources may be laborious. In some species, like leking birds (Wiley, 1973), the location of the territory relative to others may be important.

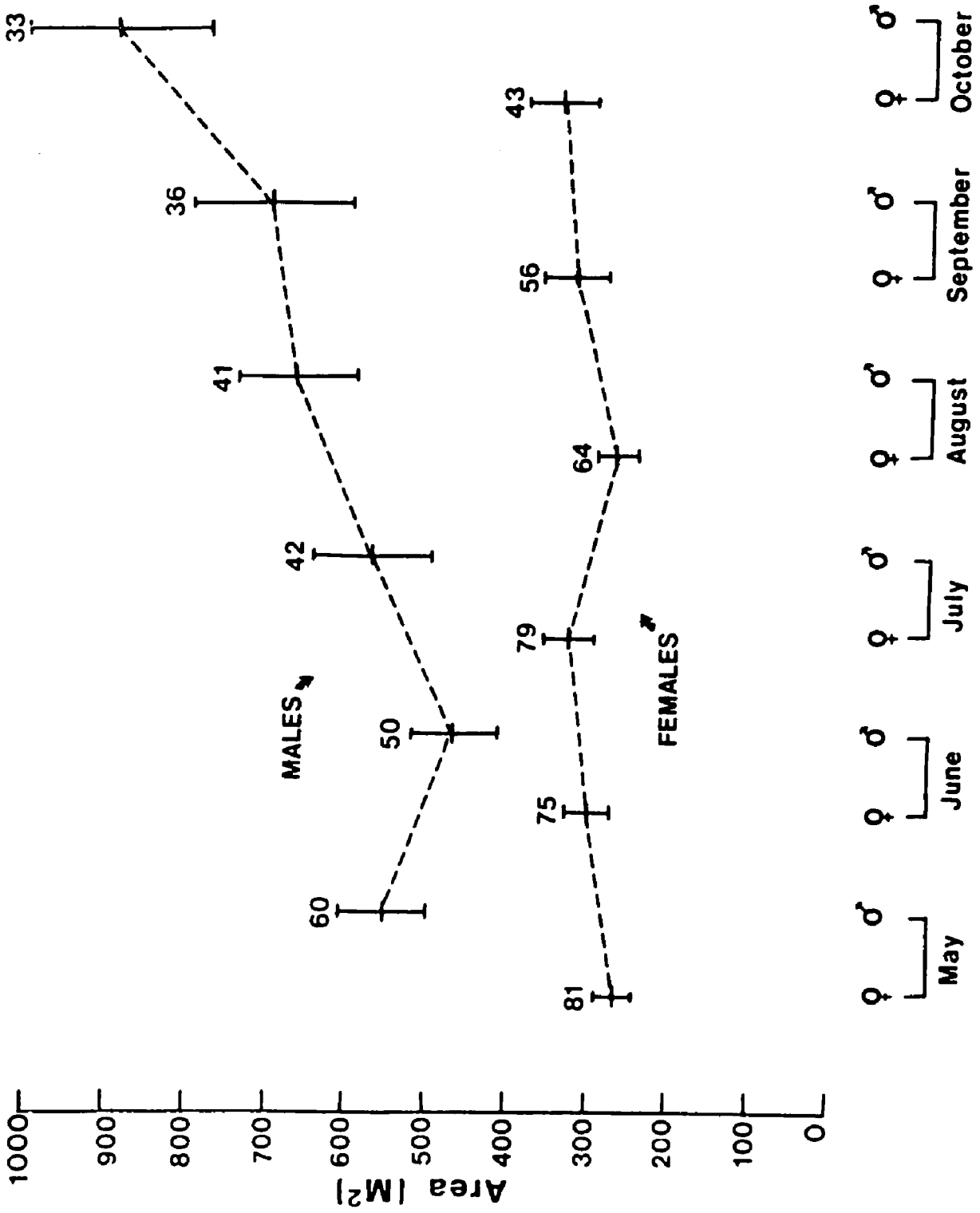
The spatial pattern of defense should be affected by the importance of the resource. Intensive defense should occur when the cost is very low (defense is cheap) or the benefit is very high (resource is very critical). When the energetic expense necessary for exclusion has an unfavorable effect upon the cost/benefit ratio, defense should be less intense and overlap with conspecifics tolerated. In this study, I measured territory size monthly, in order to obtain sufficient locations each month for delimiting territories while still keeping the interval short enough to detect changes in territory location and size.

Changes in territory size may parallel changes in aggression level. The extent of overlap between territories held by individuals of the same sex would be an indirect measure of the intensity or effectiveness of the defense. A constant aggression level when observed overlap was reduced would suggest a hypothesis that other patterns, such as activity, have changed. S. jarrovi of both sexes are territorial from May through October. Aggression data presented above indicated that an individual defended most of the area it used during a month's time for these six (May-October) months. During the rest of the year, the species is non-territorial and aggregated in large numbers for hibernation (see Chapter IV). The size of the territory increased from May to October among males (ANOVA, $p<.01$) but not among females (Figure 7). Male territories were significantly larger (t-test, $p<.01$) than female territories every month of the year. Yearly differences in means within one sex generally did not occur, except for adult male values in May. Male territories in May 1972 were significantly smaller than the values for the same month in other years (t-test, $p<.01$). This may be an artifact resulting from the later start of field work in 1972, which is more likely to underestimate the territories of males than females.

Although the average male territory increased in size during the year, not every territory expanded. Among those individuals holding territories in both June and September (N=17), no net increase occurred (Wilcoxon paired rank test,

Figure 7. Monthly territory sizes for resident adult males and females 1972 through 1974. Values shown are means ± 1 S.E. Sample sizes are indicated above each point.

Figure 7


Area (M2)
1000
900
800
700
600
500
400
300
200
100
0
MALES
FEMALES
33
36
41
42
50
60
43
56
64
79
75
81
♀ ♂ May
♀ ♂ June
♀ ♂ July
♀ ♂ August
♀ ♂ September
♀ ♂ October

$p>0.1$) since as many males decreased their territory size as increased it. The overall increase in mean territory size resulted from increased aggression (greater defense of the territory), density reductions due to predators and competitive exclusion of small males by large ones and despite partial replacement of the missing animals. Second year males with small spring territories seemed particularly vulnerable to predation or competitive exclusion by larger males. Missing individuals may be replaced by new males who defended larger territories than their predecessors because they had fewer neighbors. Males with peripheral territories in the spring may move into the more desirable central areas of the study area if the opportunity arises. The increased male territory size, which inversely correlated with male density during the year (Table 8), may partly result from reductions in encroachment pressure upon boundaries by neighboring males.

Estimates of October territories among males were larger than September (or breeding season) ones. This reflects a rather sudden loss of site fidelity after October 15 and the use of new but undefended locations. This change started at different times for particular individuals and signaled the beginning of the migration to aggregations (see Chapter IV).

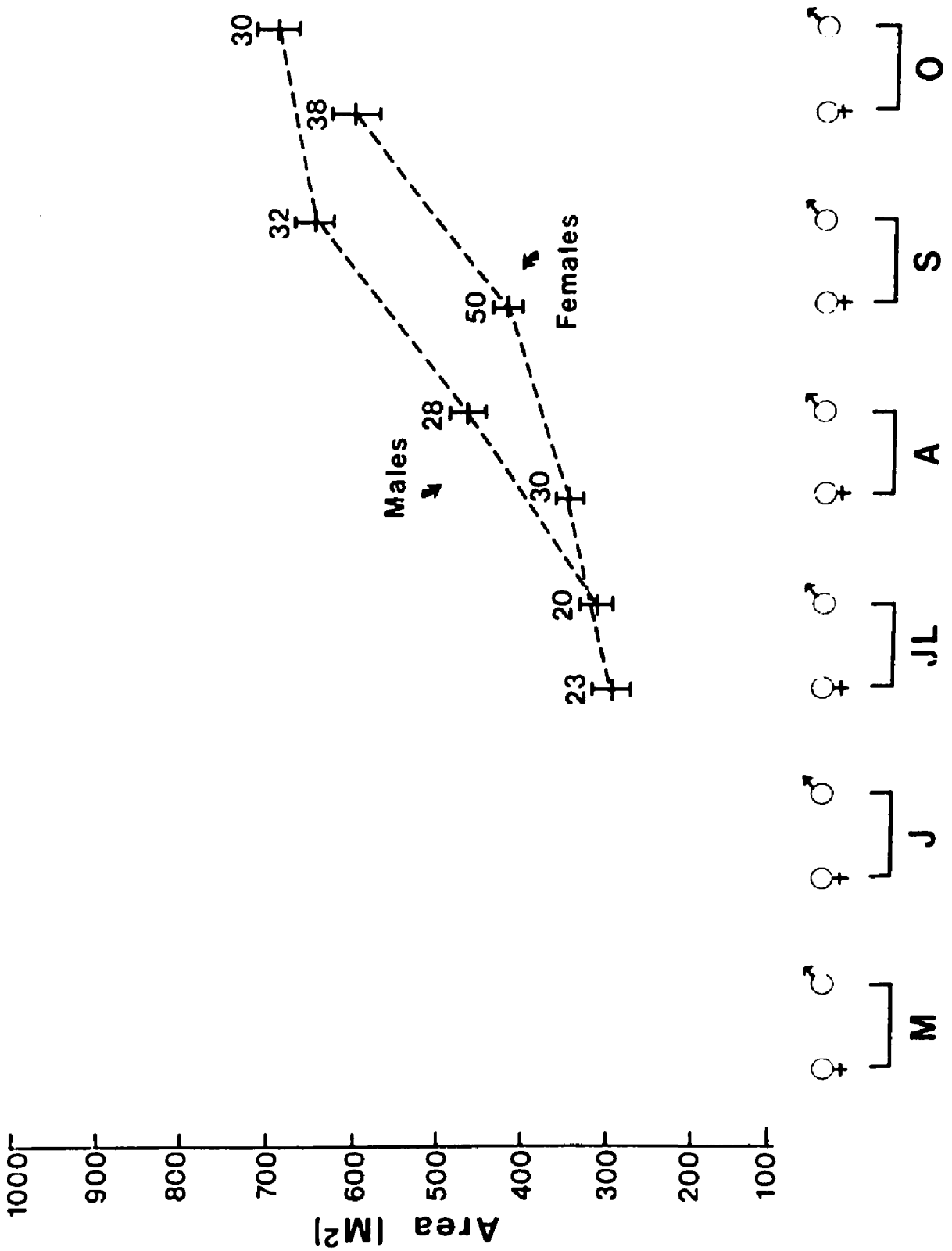
The ontogenetic events of territorial behavior were not studied in detail. Although interactions between young of either sex were observed, "territories" of young were not

defended against individuals of older age classes. Therefore, such "territories" of animals in their first growing season may be more appropriately considered home ranges. First year animals ("juveniles") did not show the strong attachment to specific locations within their area that was observed in adults. Home ranges of juveniles could not be measured with confidence prior to July. Home ranges of juvenile females were smaller (t-test, $p<.01$) than those of adults only in July. Thereafter, the size of home ranges did not differ significantly between age classes, although adult females expended more effort for defense. Home ranges of juvenile males were also smaller than for adult males in July (t-test, $p<.001$) and August ($p<.006$), but were not significantly different in size during the fall. As in females, juvenile males do not expend the energy in territorial defense that older males do. After their first July, males had larger home ranges (t-test, $p<.05$) than females of the same age (Figure 8).

Male territoriality appears advantageous for breeding, as territory size, and presumably the energy for defense, increase from May until the breeding season. The increased mean territory size results from increased aggression (Figure 2) and activity (Figure 16) of males. Some males shift their position to more desirable locations as areas are vacated due to predation and competitive exclusion. Adult females do not show seasonal changes in territory size. Juveniles occupy generally smaller home ranges which they do not defend against adults.

Figure 8. Monthly territory sizes for resident juvenile males and females 1972 through 1974. Values shown are means ± 1 S.E.

Figure 8


Area (M2)
1000
900
800
700
600
500
400
300
200
100
Males
Females
30
38
32
50
28
30
20
23
M
J
JL
A
S
O

Territorial Overlap and Hierarchial Behavior

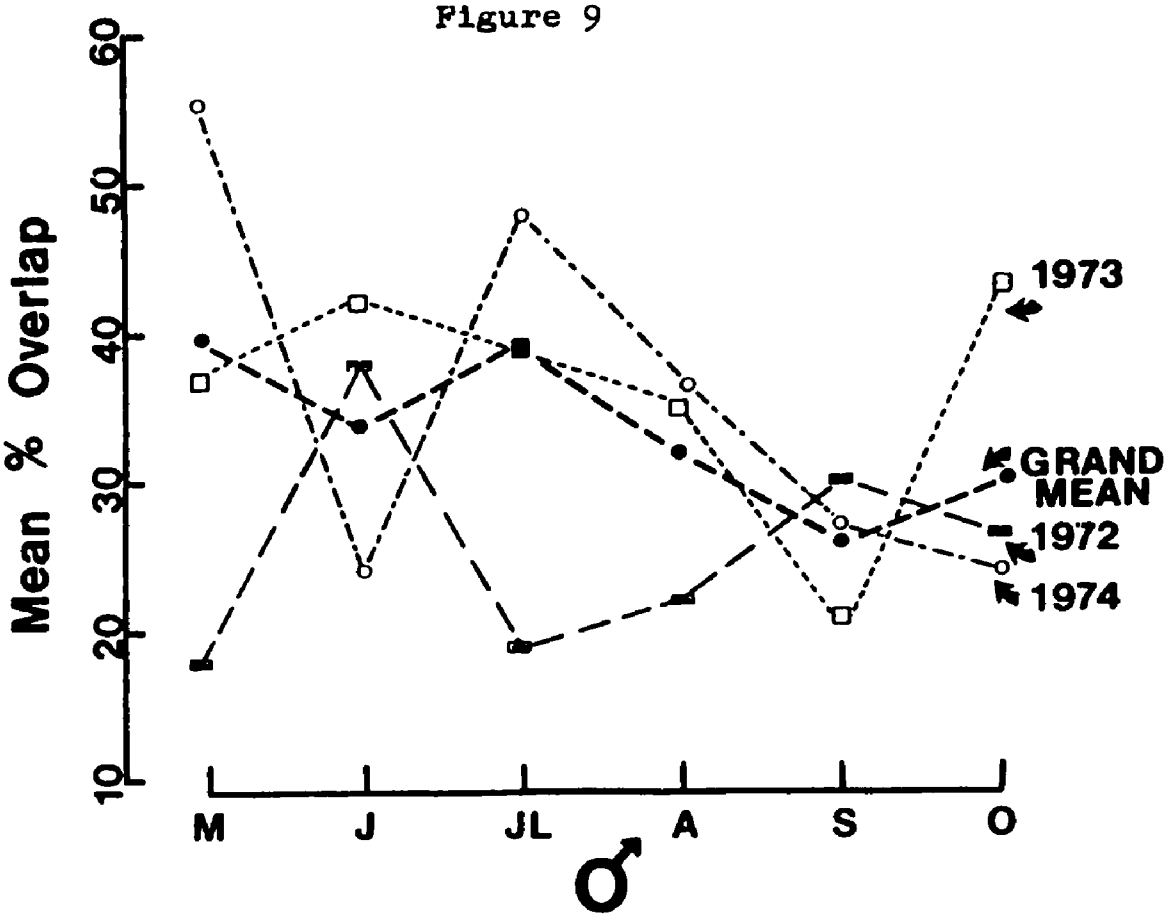
Although animals defended their surroundings, as indicated above, it may not be energetically advantageous to create an exclusive area. The degree of overlap between territories can reveal the effectiveness of territorial defense, particularly when aggression levels and territory sizes are known. If overlap is high, a potential for hierarchical behavior exists. Such situations in an otherwise territorial species may provide the adaptive context for hierarchical behavior.

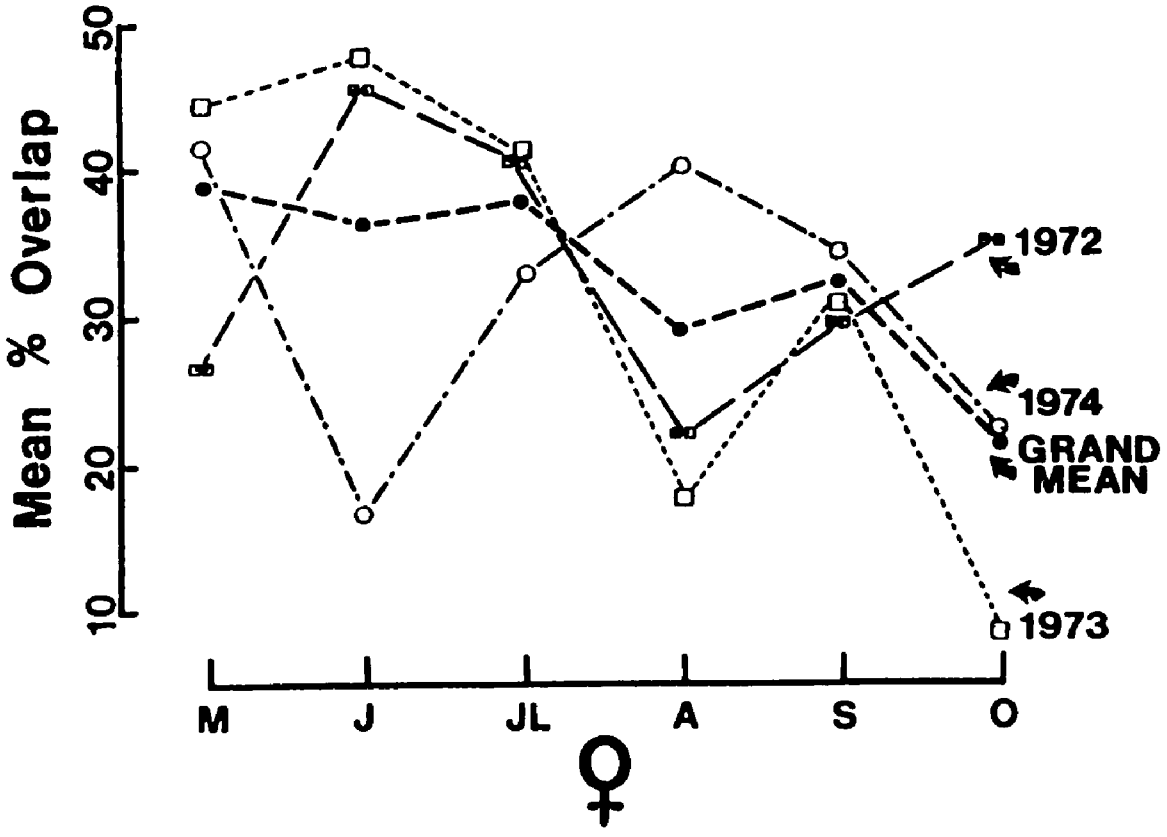
Among adult males, the pattern of territorial overlap varied widely from year to year (Figure 9). The mean overlap for all years combined is high in the spring and declines in the fall. In May, the mean territorial overlap for any year was significantly different (t-test, $p<.01$) from the values of the other two years. Sharp increases in the average overlap occurred in months when substantial numbers of migrants appeared in the study area (June 1972) or when several established male residents disappeared over a short interval (July 1974). These months were followed by periods of greatly reduced overlap as new boundaries between animals were established. A sharp drop in overlap during June 1974 seems associated with the greatly reduced activity of males during that month (see Figure 14), probably resulting from the extremely high temperatures and very dry conditions then.

During the breeding season (September 15-October 15), male-male aggression reduced the degree of territorial overlap between males to a minimum value which was

Figure 9. Extent of territorial overlap between adults of the same sex 1972-1974. The grand mean is the weighted value of all observations.

Figure 9


Mean % Overlap
60
50
40
30
20
10
1973
GRAND MEAN
1972
1974
M
J
JL
A
S
O
♂


Mean % Overlap
50
40
30
20
10
1972
1974
GRAND MEAN
1973
M
J
JL
A
S
O
♀

approximately the same for each year. Increased aggression and vigorous territory patrolling from late August to mid-October contributed to this exclusiveness of area. The mean value does not reach zero during the breeding season because older males tolerated some overlap with second year males. The similar values in different breeding seasons suggest this average overlap may represent the balance point between defense costs and reproductive benefit.

Female territorial overlap also declined gradually during the year but varied less between years than did that of males (Figure 9). Two sharp drops (October 1973 and June 1974) occurred in months when female activity levels were greatly reduced (see Figure 15). The apparent increases during July and August 1974 seem related to shifts toward the center of the study area by many females.

The aggression-body size relationship discussed above (see Figures 4 and 5 for examples) gave a competitive advantage to the larger and generally older individual who occupied the overlapping area. Because pursuit at the end of encounters was generally short, a "loser" was rarely chased completely out of the "winner's" territory. Some smaller animals remained in the dominant's territory and overlaps persisted. However, repeated encounters between individuals caused the smaller animal to leave the area or to give the dominant a very wide berth.

Dominance behavior appeared most clearly in the relationship between different age-classes of males. Only

one animal older than two years displayed persistent subordinance. Thirty second-year males had territorial overlaps of at least 45% with other males in one or more months. Overlaps were most frequent in the spring and summer but some cases occurred in or persisted until fall when vacant areas were presumably available but not used by the subordinate male. The subordinate generally fled if the dominant approached.

First-year males were always subordinate to any older male. During the summer, first-year animals avoided older animals although they rarely displayed overt aggression. In late August, older males began attacking yearling males as breeding activity (persistent courtship of females) started and they attained mature size and adult throat colors (dark blue). First-year males usually persisted in an area despite the older male's persecution by avoiding the older animal.

The relative merits of submissive behavior versus migration cannot be determined from this study. A few individuals, which were driven from the study area by a larger animal, reappeared during the subsequent spring and established territories. This suggests an alternative to submissive behavior does exist. The importance of conditions favoring one or the other strategy, such as the probability of finding an unoccupied site and the degree of tolerance by older males, can only be speculated upon from existing data.

Aggressive behavior broke down completely in one context. When the rainy season began in July, feeding aggregations of up to ten lizards (all S. jarrovi) developed at sites with Isoptera or Hymenoptera swarms. The congregating sites were large rocky areas lacking vegetation. Aggregations lasted one or two hours in the morning with little overt aggression between individuals as each darted from place to place catching insects. When the insect swarms thinned and feeding rates slowed, the largest males began interacting, creating chain reactions. The smaller animals retreated and displayed at another individual, thus breaking up the aggregation.

The high values of territorial overlap between males during a month, particularly in the spring and summer, and observations of encounters between overlapping individuals suggest two-rank dominance relationships occur with some frequency. As the fall breeding season approaches, overlap is reduced due to increasing aggression and encounter frequency among males. Because the reproductive gain has increased, males compete more intensely in the fall for areas containing females. Females also overlap broadly despite their smaller territory size. Dominance relationships were poorly defined among females.

Selection of Territorial Site

Organisms are unevenly distributed in their habitats thus utilizing the patchiness of optimal microhabitats. If the cues for territorial site selection can be elucidated,

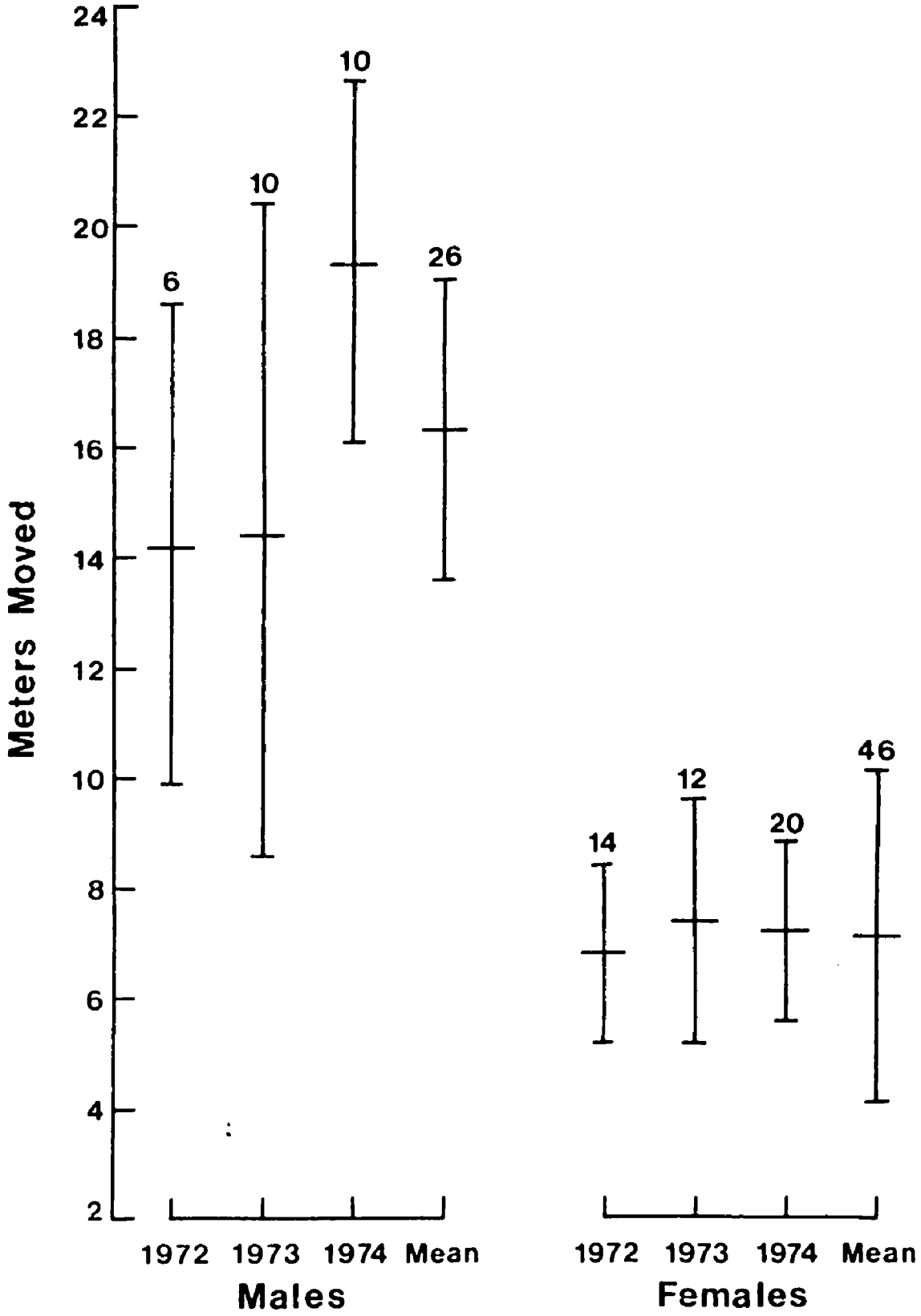
the resources for which defense is advantageous may be identified. Differences between the sexes may be particularly important. The greater investment in the offspring by the female should make her more sensitive to food resources than the male, unless his aggression and mate-seeking activities are equally energy consuming (see Figure 16).

The time delay between spring dispersal from hibernation (Burns, 1970) and fall breeding in S. jarrovi makes it likely that the location for maximal reproductive success may be difficult to predict in the spring. Females should choose areas with the highest food value over the warm months (May-October). In contrast, males should select sites containing the maximum number of defendable females.

The extent of site fidelity, measured as the distance between individual activity centers from May to the breeding season, estimates the animal's ability to predict good breeding sites in the spring. Females are more conservative in this regard as males shifted significantly further (t-test, $p<.01$) than females in all three years (Figure 10). The male shift did not correlate with the seasonal increases in territory size and was not an artifact of the increasing mean size of male territories during the year. In contrast, the extent of shifting in females correlated positively with breeding season territory size ($p<.001$) despite the smaller range of sizes. It appears that females selected year-long territorial positions in May and males shifted territorial locations during the year. The criteria for

Figure 10. The distance that activity centers of adults moved from May to the breeding season (September 15 - October 15). Values shown are means ± 1 S.E. Sample sizes are given above each figure.

Figure 10


Meters Moved
24
22
20
18
16
14
12
10
8
6
4
2
6
10
10
26
14
12
20
46
1972
1973
1974
Mean
Males
1972
1973
1974
Mean
Females

establishment of a territory may differ between the sexes. Females use some factor or factors present in the spring but probably not the quality of the male at a particular site. Males delimit their territories later in the year on the basis of female dispersal.

I attempted to correlate female densities at 30 circular areas with environmental conditions at each site. The locations are shown in Appendix II. Since this species prefers rocky habitats, predictably the extent of rocky substrate within each location correlated significantly (t-test, $p<.05$) with adult female density (Table 4). The number of crevices within each area was much less valuable, correlating significantly in only two trials.

Higher female densities should occur at locations with high food values. Simon (1975) related territory size in S. jarrovi to food abundance. My data indicated that food values (numbers of insects captured on sticky traps) did not correlate with female density at the 30 locations on any date. Food values at a particular location correlated significantly ($p<.05$) between pairs of dates in only two of 15 comparisons (Table 5). In the two June trials, food values were so low (range 0-7 items/trap) that differences between traps could have occurred due to chance. Logistic difficulties prevented the start of the experiment in May, which seriously weakens any possible conclusions about the importance of early spring food distribution upon site selection.

TABLE 4

CORRELATIONS BETWEEN FEMALE LIZARD DENSITY, EXTENT OF ROCKY SUBSTRATE, AND NUMBER OF CREVICES FOR SIX PERIODS DURING 1974.

Date of Trial	Rockiness	Crevices
June 6	.6324**	.4605*
June 22	.5630**	.2941
July 10	.5063**	.3525
July 30	.3958**	.3958*
August 19	.4301*	.1595
September 24	.1492	.3574

* = Significance at 0.05 Level

** = 0.01 Level

I tested whether some degree of predictability in food values may occur over the entire year. Insect numbers caught on each trap on the July 30, August 19 and September 24th dates correlated significantly ($p<.05$) with the average food value for that location (Table 5). Since collections on July 30th were 46% of the total food items counted during 1974, this strong correlation ($r=.8433$, $p<.01$) was expected. Food values for traps during the August and September trials were highly correlated with the average value per trap (August $r=.4992$, $p<.01$; September $r=.5010$, $p<.01$) although fewer insects were collected each time. Further data collection would be required to substantiate whether this temporal pattern occurred every year.

Food abundance seems dependent upon rainfall. The average number of food items captured each date during 1974 corresponded closely with the rainfall pattern (Figure 11). Support for this relationship comes from unpublished data generously supplied by Royce Ballinger who performed similar food studies in the Chiricahua Mountains, approximately 100km southeast of the Pinaleños, at comparable elevations during 1973 and 1974. The two data sets show some similarities. Food levels fluctuate during the year with sharp rises in food abundance in July with the onset of summer rains. Spring food levels may be especially variable from year to year, depending upon the amount of snowfall (winter precipitation). The higher values in June 1973 compared to those in June 1974 may result from the greater precipitation

TABLE 5

CORRELATIONS BETWEEN FOOD VALUES AT 30 LOCATIONS

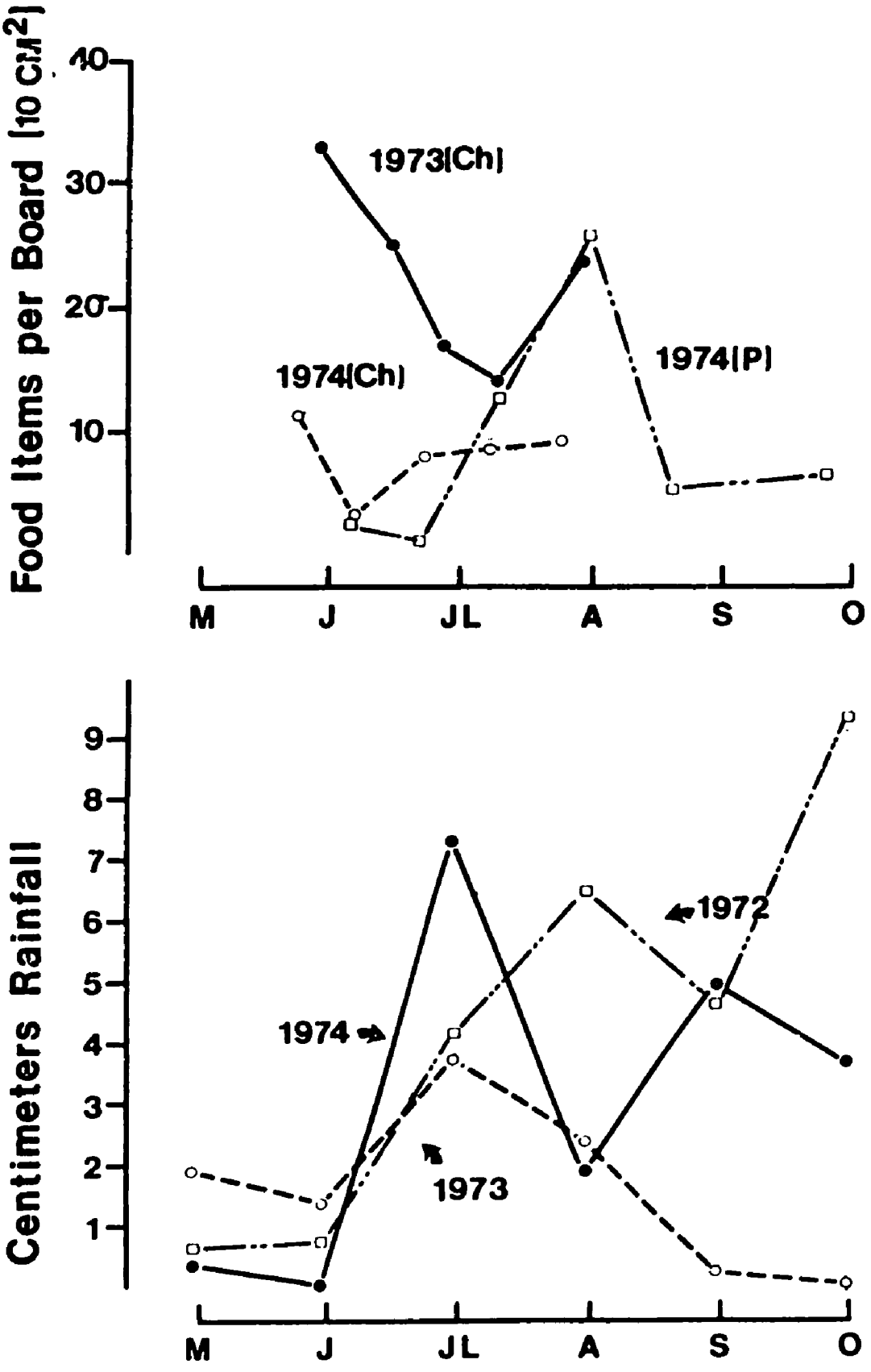
IN THE STUDY AREA FOR SIX DATES AND THE AVERAGE VALUE.

Trial	June 6	June 22	July 10	July 30	August 19	September 24
June 6	1.00					
June 22	.1523	1.00				
July 10	.0923	-.0613	1.000			
July 30	-.2671	.0932	-.1093	1.000		
August 19	.4307*	.2082	.3714*	.2463	1.000	
September 24	.0092	.1558	.2436	.1690	.0067	1.000
Average food value	-.0384	.1953	.3320	.8433*	.4992*	.5010*

* = Significance at 0.05 level.

Figure 11. The relationship between insect abundance and monthly rainfall. The symbols (CH) and (P) represent data from the Chiricahua and Pinaleño Mountains of Arizona, respectively. Chiricahua data generously supplied by Dr. Royce Ballinger. Rainfall records were taken from the weather station at Safford, Arizona, the closest one to the study area in the Pinaleños.

Figure 11


Food Items per Board (10 CM2)
40
30
20
10
1973(Ch)
1974(Ch)
1974(P)
M
J
JL
A
S
O
Centimeters Rainfall
9
8
7
6
5
4
3
2
1
1972
1974
1973
M
J
JL
A
S
O

in the winter 1972-73 as compared to 1973-74 (Appendix I).

Locations in the center of the study area were desirable over periphery sites. This results from the moister conditions in the center, which presumably correlate with insect abundance. Food items on the periphery of the study area were significantly more scarce during the first July run (ANOVA, $p<.02$) and in September (ANOVA, $p<.02$) compared to central locations. Values did not differ between the center and the periphery in the other four trials. The differences in insect distribution during early July and September suggest an advantage accrues to animals with centrally located territories as food values are high for a longer period of time. However, total counts of insects for all six dates do not show clear unimodal (central) tendencies along transects (Figure 12).

Behavioral characters were also investigated for correlation with female distribution. Presence of and interaction with a male were not important requirements to females since only 66% of the females in either age category (N=95) overlapped with males in May (Figure 13). A higher percentage should be expected if males entered into female site choice, especially considering the larger size of male territories.

Examination of female-female overlap indicates age classes differ in their overlap patterns. Second year females show no preference for overlapping with females of the same or the older age class (Table 6A). Older females appear to prefer overlapping with females of the same age. However,

Figure 12. Total numbers of insects captured at 30 locations in the summer site during 1974. Each letter (A through E) represents one transect of six traps.

Figure 12

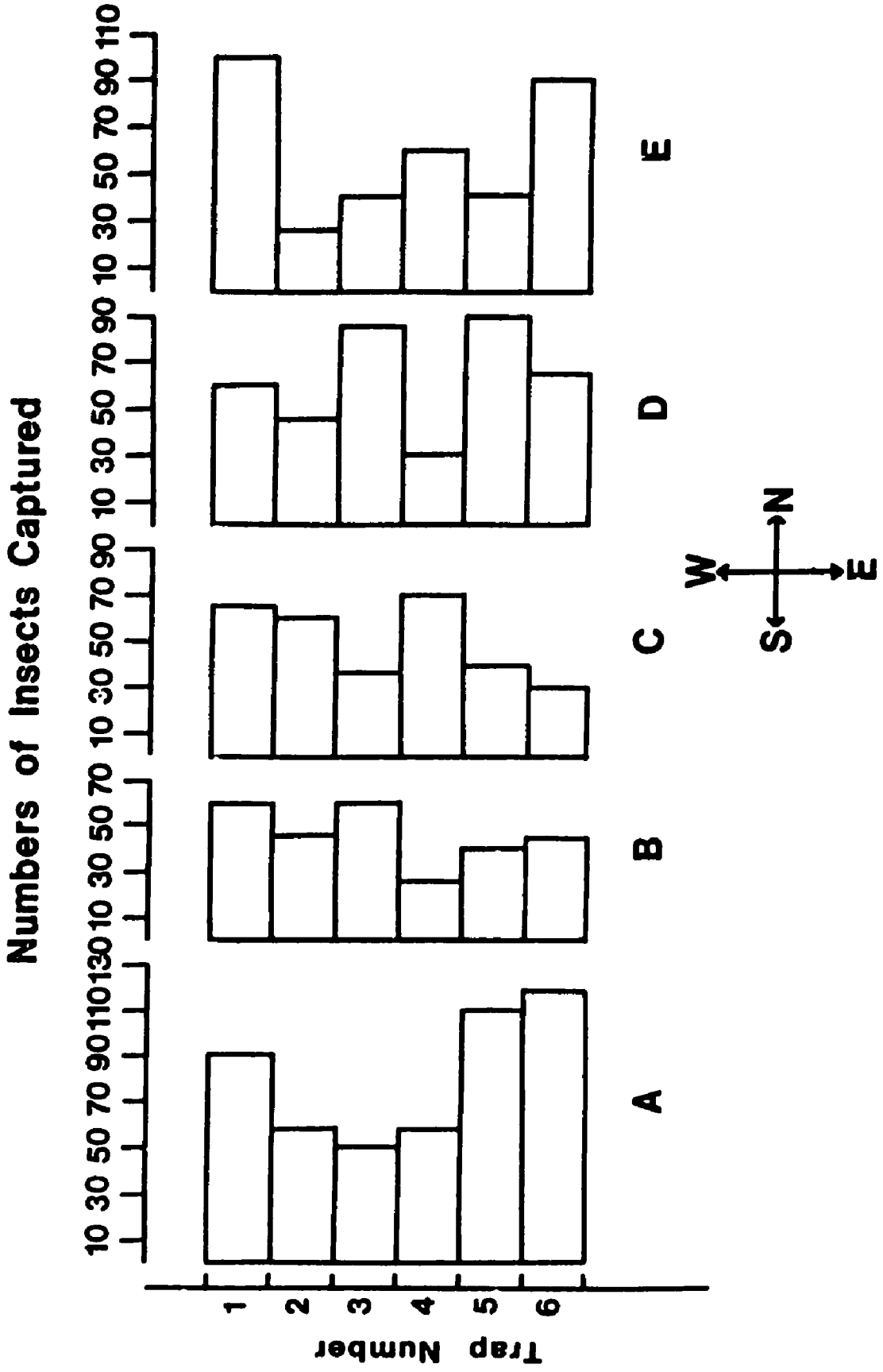

Numbers of Insects Captured
10 30 50 70 90 110
10 30 50 70 90 110
10 30 50 70 90 110
10 30 50 70 90 110
10 30 50 70 90 110
A
B
C
D
E
1 2 3 4 5 6
Trap Number
N
W
E
S

Figure 13. The degree of territorial overlap by resident adult females with males, other females and the October territory used previously. The May territory was used for comparisons. Two age classes of females are identified. Criteria for overlap is given in the text.

Figure 13

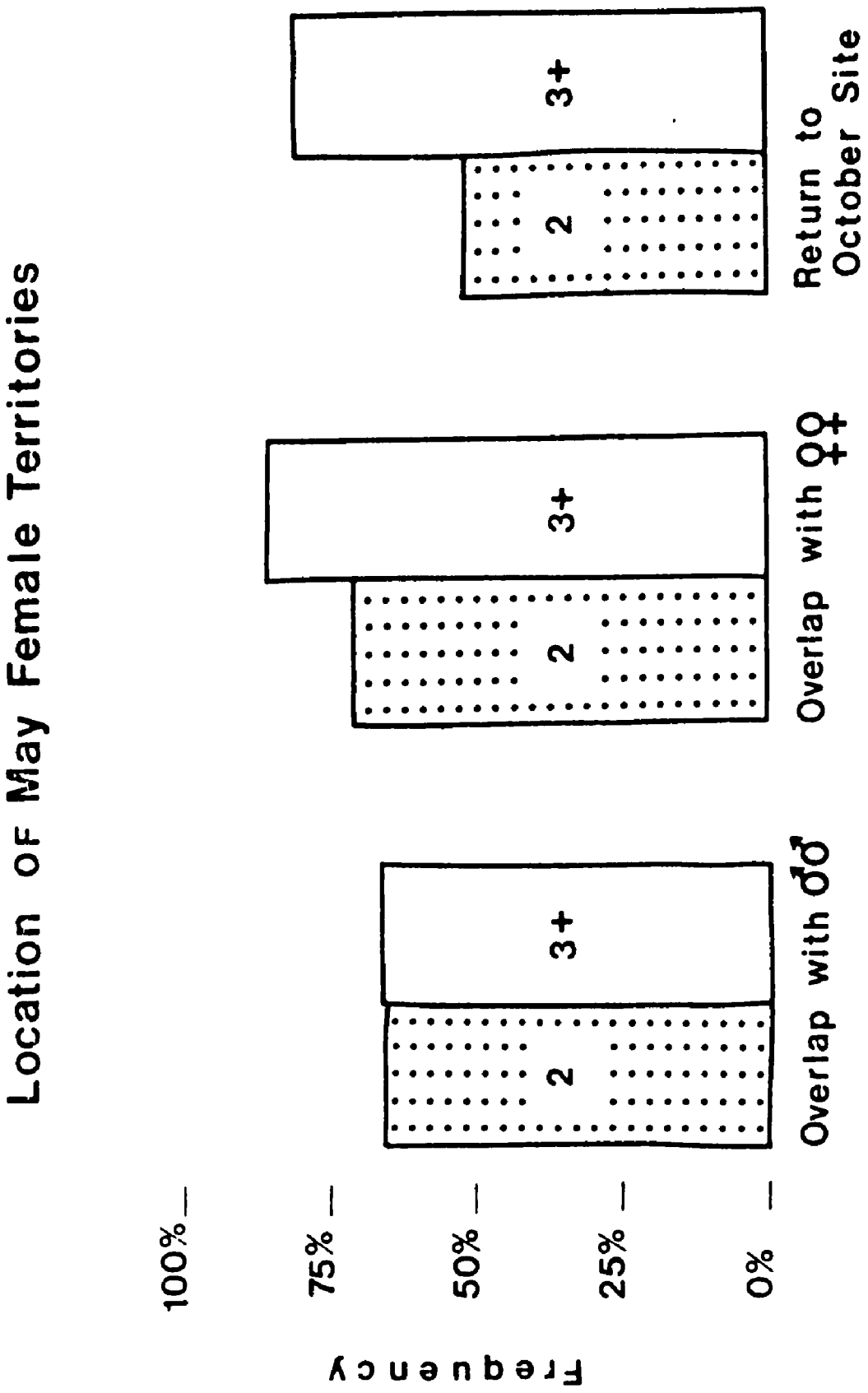

Location of May Female Territories
Frequency
100%
75%
50%
25%
0%
3+
2
Overlap with ♂♂
Overlap with ♀♀
Return to October Site

TABLE 6

OVERLAP PATTERNS OF ADULT FEMALES IN MAY

A. The presence of other individuals

	territorial overlap with:		
	males	2nd yr females	3rd yr females
Second year females (N=52)	67%	37%	48%
Older females (N=43)	66%	47%	72%

B. Preference for own age class

	territorial overlap with:		
	only 2nd yr female	only older female	both age classes
Second year females (N=52)	13%	29%	19%
Older females (N=43)	26%	42%	29%

C. Extent of overlap between females

	None	light (<30%)	medium (30-60%)	heavy (>60%)
Second year females (N=52)	15 (29%)	7 (13%)	12 (23%)	18 (35%)
Older females (N=43)	6 (14%)	5 (12%)	15 (35%)	17 (40%)

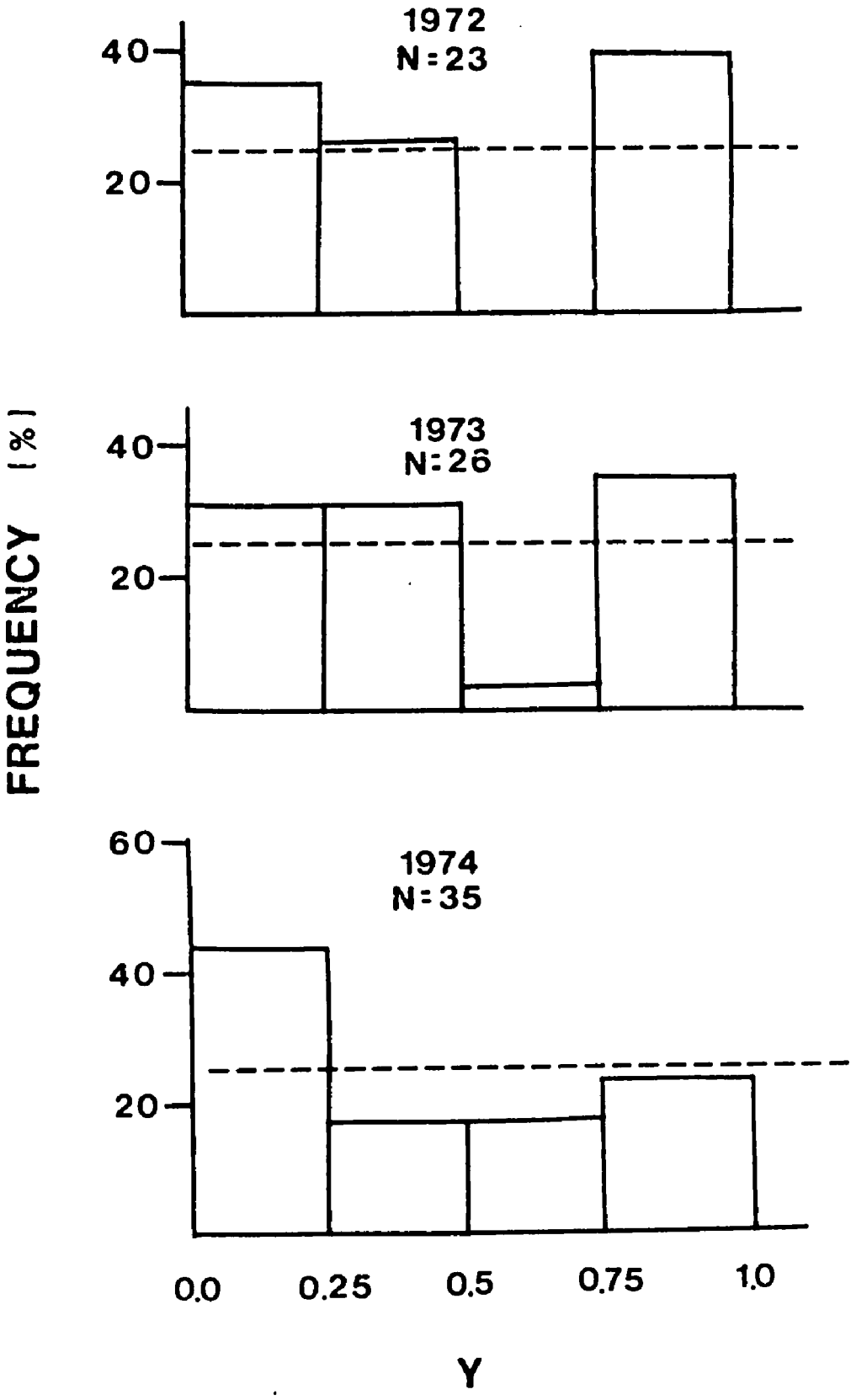
when the overlap pattern is further broken down (Table 6B), there are no differences between the female age classes (χ^2 test, $0.1>p>.05$). When the degree of female-female overlap is quantified into four categories (Table 6C), second-year females overlap any female significantly less frequently ($\chi^2=20.89$; 3 df; $p<.01$) than do older females. However, if nonoverlapping females are excluded from the analysis of overlap patterns, there are no age class differences. In both age groups, the frequency of individuals within a category increases as the degree of overlap increases. This distribution is significantly different from one of equal proportions per category ($\chi^2=11.06$; 2 df; $p<.01$). However, it is unknown what overlap patterns would be generated by random distributions.

I tested for female clumping by using nearest-neighbor analysis (Pielou, 1962). I calculated the distance for each female to its nearest female neighbor, using activity centers to represent the location of females. The distribution of distances for each May is shown in Figure 14. The 1972 distribution is significantly different (χ^2 test, $p<.05$) and the other years insignificant ($p>0.1$) from a random distribution. Considering the limitations of the test due to sample sizes and the marginal significances of overlap patterns and nearest-neighbor analysis, it is not possible to demonstrate conclusively that females clump.

Females in the two age classes also show different degrees of site tenacity to the October territory (Figure 13). Seventeen of 35 (48%) second-year females abandoned their

Figure 14. The distribution of nearest neighbor distances between females in May. Activity centers represented the location of each female. The dashed line represents the expected distribution when values are transformed by the method of Pielou (1962).

Figure 14


1972
N=23
40
20
1973
N=26
40
20
1974
N=35
60
40
20
FREQUENCY (%)
0.0
0.25
0.5
0.75
1.0
Y

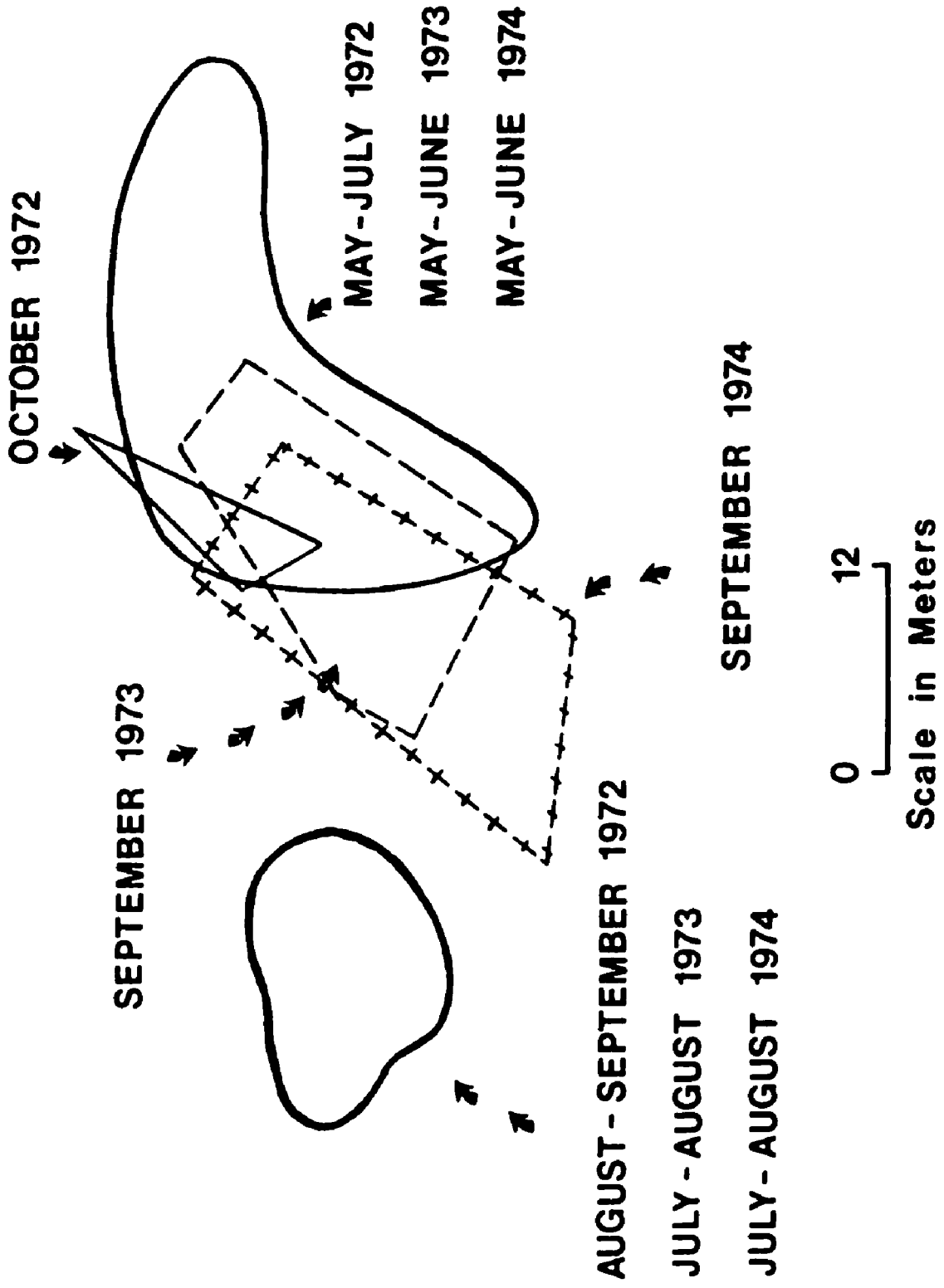
October site whereas only four of 25 (16%) older females did so. Most second-year females which moved chose locations greater than 10m from their October site. The four older females were all near, although not overlapping, their October territory.

There were exceptional females that were not sedentary. One adult female regularly changed the position of her territory each season (Figure 15). A remarkable pattern emerged over the three years for this female. She stayed in the study area center until after parturition, then moved each summer onto the western hill beyond the study area boundary. During the breeding season each year, the female reappeared in another part of the study area and mated with the resident male of that area.

Habitat selection in females involves territorial establishment in May. The male decision to settle is postponed until later in the summer. It was not possible to identify conclusively which factors influence female distribution in the spring. The extent of rocky substrate, some aspect of food predictability and perhaps the presence of other females may enter into the female's choice. The higher than expected clumping among females suggests there is some attraction to sites which contain females. However, the differences in overlap pattern between female age classes and the aggressiveness between females (Figures 3 and 5) suggest that the clumping is correlated with environmental factors other than attraction between females.

Figure 15. An exception to the generally sedentary female. Territorial areas for one adult female during 1972 through 1974 are shown. Spring and summer areas have been simplified for clarity.

Figure 15


OCTOBER 1972
MAY-JULY 1972
MAY-JUNE 1973
MAY-JUNE 1974
SEPTEMBER 1973
AUGUST-SEPTEMBER 1972
JULY-AUGUST 1973
SEPTEMBER 1974
JULY-AUGUST 1974
0
12
Scale in Meters

Activity Patterns

Animals allocate energy in ways that are presumably adaptive. Assuming the energy available to an individual is limited, trade-offs in the energy allocations for various activities must be made. Several sexual differences in behavior already discussed have suggested that females expend less energy in territorial activities than do males. This occurs presumably because females apportion more energy to their gametes than do males. Measures of activity will enable quantification of the energy expended by males, which may equal female expenditures but is alloted to different activities.

Territory size is an indirect measure of activity, as observations of more active animals are more likely to encompass the entire territory. However, the correlation between activity and territory size may not be close. The relationship would be complicated by feeding patterns and the ability of the animal to detect and repeal intruders. Defense of an expanded territory should always produce increases in activity but greater activity may not always result in larger territories. Greater activity without territory expansion should reduce the extent of overlap because the perimeters would be patrolled more frequently.

Activity was measured as frequency of daily sighting and distances individual animals moved. Varying levels of daily sightings have been previously reported for S. jarrovi during the warm months (Simon, 1973). Despite persistent efforts, I was not able to locate all individuals each

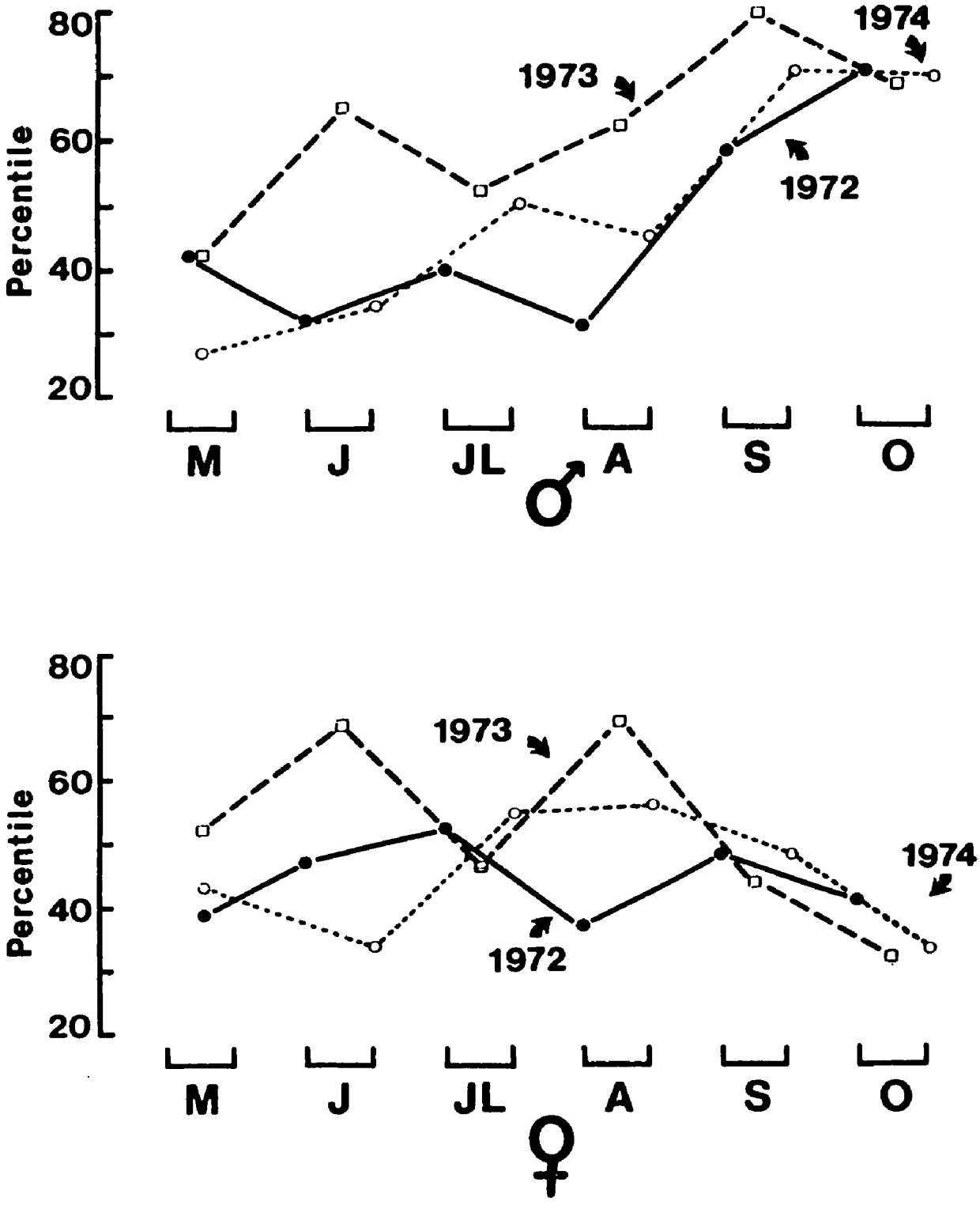
observation day. During the hottest weather (late May- early July), one or two sightings per week were typical for many individuals. As less desirable habitat surrounded the study area, I doubt that wanderings of animals in these areas resulted in their omission from the weekly census. Searches in the peripheral areas at irregular intervals failed to locate missing animals. A tendency to be arboreal (Burns, 1970) or restricted to crevice openings during the hottest weather may reduce the frequency of sightings. No individual was seen higher than three meters in a tree.

The mean frequency with which adults were seen during the six months of activity (May through October) is shown in Figure 15. Females were more active than males in June 1972, July 1972, May 1973 and May 1974, but only in June 1972 and May 1974 were the differences significant (t-test, $p<.05$). In contrast, males were significantly more active ($p<.05$) in September (1973, 1974) and October (1972-74) than females. The fall difference in activity is the result of both increasing male activity and declining female activity. Males actively search for females during the fall months and engage in conspicuous behavior. The consistency between years suggests that the sexual difference in activity has a biological basis.

More quantitative estimates of energy expenditures can be obtained from the distance animals moved hourly during daily activity periods. Data were gathered in 1973 and 1974. During May, August, and September 1973, males traveled greater distances per day than females. However, sufficient

Figure 16. Activity levels (frequency of daily sightings) for adult residents. The mean value for each month is shown.

Figure 16


80
60
40
20
Percentile
1974
1973
1972
M
J
JL
A
S
O
♂
80
60
40
20
Percentile
1973
1974
1972
M
J
JL
A
S
O
♀

observations in the afternoon during 1973 could not be obtained for most months. This difficulty can be attributed to the particularly hot, dry weather during the summer of 1973 (Appendix I). I suspect that the scarcity of animals in the afternoon was a response to the stressful weather conditions. In September, when the data were most complete (Table 7), males moved further than females in six of seven hourly periods during the day (t-test, $p<.05$). No data for females could be obtained in October so no comparison could be made between sexes.

More complete data were obtained in 1974. For each month, the total distance moved in a day (the sum of the hourly means) was greater for males than for females (Figure 17). Females showed greater hourly movement than males only once (July, 1000-1100) during the entire year. Males were more active for three hourly periods during the summer months. However, in September and October, males were more active than females in six of the seven hourly periods of activity (t-test, $p<.05$), in agreement with the September 1973 data. The increases in territory size and the reductions in territorial overlap during the breeding season may result from this increased activity by males.

The consistent sexual difference in territory size was not correlated with sexual distinctions in activity until the fall breeding season. This suggests that the sexes covered an area (foraged?) in different ways. In addition, the sharp increase in male movement between August and September did not produce an equally dramatic increase in

TABLE 7

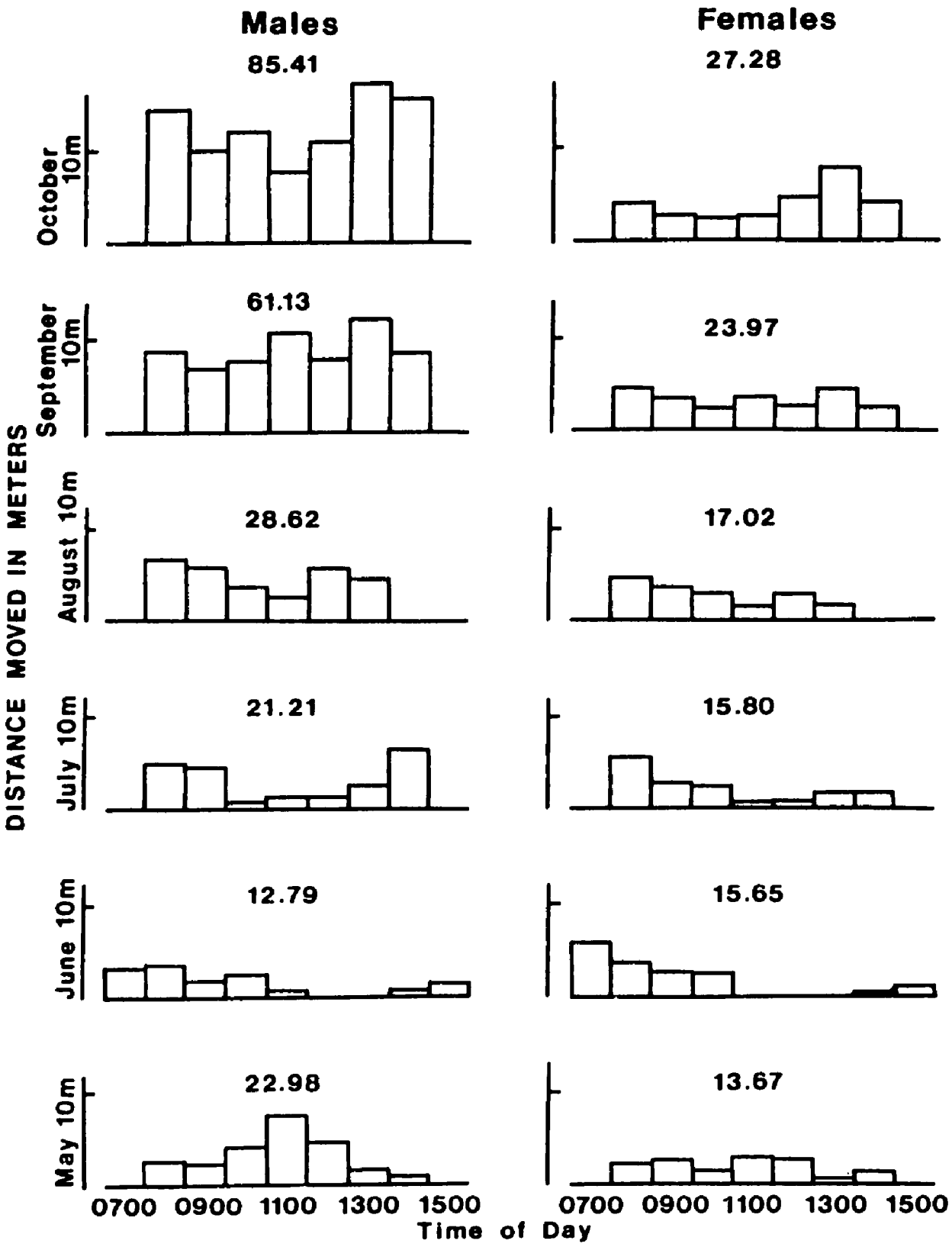
MOVEMENT PER HOUR BY ADULTS DURING SEPTEMBER 1973.

Time	Males	Females	Sig.
8-9	9.34 ± 9.26 m (38)	3.51 ± 4.15 m (20)	<.01
9-10	7.29 ± 6.85 (43)	2.65 ± 0.30 (23)	<.01
10-11	5.55 ± 5.57 (41)	1.98 ± 2.20 (20)	<.01
11-12	5.22 ± 5.39 (22)	2.59 ± 2.03 (8)	<.05
12-1	2.98 ± 2.99 (9)	3.35 ± 2.16 (2)	NS
1-2	9.38 ± 11.50 (17)	2.59 ± 1.63 (8)	<.05
2-3	8.56 ± 7.81 (13)	1.44 ± 1.14 (7)	<.05

VALUES ARE MEANS ± 1 S.E.
PARENTHETICAL VALUES ARE SAMPLE SIZES

Figure 17. Distance moved per hour by adults during each month in 1974. Numbers above each histogram represent the sum of the hourly means.

Figure 17


Males
Females
85.41
27.28
October 10m
61.13
23.97
September 10m
28.62
17.02
August 10m
21.21
15.80
July 10m
12.79
15.65
June 10m
22.98
13.67
May 10m
DISTANCE MOVED IN METERS
0700 0900 1100 1300 1500
0700 0900 1100 1300 1500
Time of Day

territory size. The increased activity did result in reduced male-male territorial overlap.

The 1974 data showed the activity pattern was not consistently unimodal or bimodal during the year. Unimodal activity was apparent in May and in the fall, but activity was bimodal June through August. The increasingly earlier peak of activity in June and July occurred because animals emerged earlier and avoided the hot times of the day. In June, some animals emerged from their crevices before sunlight had penetrated the canyon floor. Summer observations of activity were made with the least effort prior to 1100 hours each day. Although precise hourly counts could not be taken, it appeared that fewer animals were above ground from 1100 to 1400 hours compared to other times of the day during the hot months. This impression may result from the reduced activity of individuals during this period (Figure 17) and from animals selecting more shaded, less conspicuous locations.

In general, annual activity patterns differ between the sexes. Both measures of activity (daily sightings and distance moved) increase sharply in males during the fall breeding season over summer levels. In contrast, females show no changes or else display reduced activity during the breeding season. In the spring and summer, both sexes avoid the hotter times of the day with the morning activity peak shifting to earlier hours as the maximum daily temperatures rise.

Density

A number of studies suggest density-dependent changes in the behavior of lizards (see Brattstrom, 1974 for review). Significant changes in density could influence interpretations of aggression and territorial behavior. While no efforts were made to control density during the study, population levels did not change significantly between years.

Monthly density estimates of adults and young for each month are shown in Table 8. Each year, the adult population peaked in the spring and declined to a lower but relatively stable level each fall. As indicated by the recruitment data (Table 9), more new individuals, other than newborn young, enter the study area before August 1 than after that date. Subsequent drops in density result from mortality losses as both sexes decline in numbers and from the apparent exclusion of some males, based on the sex ratio data of particular age classes, (see Figure 5). The skewness in sex ratio among second-year animals suggests that males of this age class are being (1) evicted from the study area by larger and older males or (2) suffer greater predation rates that are associated with poorer areas. One would expect marginal areas outside the study area to contain more young males than would be expected by chance alone if behavioral exclusion was a significant factor. Because of the irregularity of searches through the boundary areas, this expectation cannot be supported by the existing data.

Because density levels were similar each year and consistently declined during the warm months of each year, interpretation of the observations on aggressive and territorial behavior reported here are not complicated by apparent density effects.

TABLE 8
MONTHLY NUMBERS OF RESIDENT MALES AND FEMALES
1972-74. (PER 0.60 HECTARE STUDY AREA.)

Month	Male			Female		
	1972	1973	1974	1972	1973	1974
May	20	22	20	31	29	30
June	21	18	14	32	23	21
July	18	16	17	29	21	27
August	12	13	14	26	14	24
September	10	12	10	22	15	18
October	8	12	10	19	11	17

	Male Young			Female Young		
	1972	1973	1974	1972	1973	1974
May	--	--	--	--	--	--
June	2	--	--	7	--	--
July	4	6	10	7	9	7
August	10	8	10	11	15	4
September	10	11	12	12	23	9
October	9	13	8	8	19	11

TABLE 9

THE NUMBER OF NEW ANIMALS MARKED EACH MONTH

IN THE SUMMER SITE 1972-74

Month	Adult Males			Adult Females			Young		
	72	73	74	72	73	74	72	73	74
May	-	2	4	-	1	3	16	-	1
June	2	0	1	3	1	2	22	8	10
July	2	2	4	2	0	4	12	32	17
August	0	0	1	1	1	1	7	22	10
September	0	2	4	0	3	1	7	13	8
October	0	5	1	0	0	0	3	15	4

DISCUSSION

Changes in the behavior of lizards have been identified with climatic regimes, either hot/cold (Worthington and Sabath, 1966; Weintraub, 1968) or wet/dry (Sexton et al., 1971; Andrews, 1971; Fleming and Hooker, 1975). The seasonality of tropical breeding cycles has been correlated with the severity of the dry season (Licht and Gorman, 1970). Seasonal behavior patterns which result from breeding activity rather than climatic conditions have rarely been quantified in lizards (Yedlin and Ferguson, 1971; Ferner, 1974). Reduced activity after the breeding season has been reported in some temperate zone lizards (Fitch, 1940; Stebbins, 1944; Spoecker, 1967; Berry, 1974). Territory size declined after breeding in Sceloporus undulatus (Ferner, 1974). The absence of territoriality and breeding activity in Sauromalus during a stressful year (Berry, 1974) further supports a hypothesis that male territoriality is adaptive to their reproductive success.

Some lizard species do not show seasonal variation in aggression. Fighting in Anolis lineatopus remains at a nearly uniform level all year (Rand, 1967). Territorial defense in Sceloporus merriami (Milstead, 1970) and S. graciosus (Ferguson, 1971) is high in August, about two or more months after the breeding season. Selective factors that favor constant over varying aggression are unknown.

Behavioral patterns are simpler in female S. jarrovi than in males and show less seasonal variation. It is likely, therefore, that females are responsive to food resources and males are most sensitive to distribution of females. Females did not vary during the year in the frequency of intrasexual encounters or in territory size. Less change in display intensity frequency occurred in females than in males. However, female displays during natural encounters in the summer were more intense than those in the spring or fall. This seasonal shift and the differences between years in female responses to introduced males contradicted this picture of constant female aggression. Relative constancy of female intrasexual aggression may result from constant factors, interactions which remain in equilibrium or selection for an average but most adaptive aggression level.

The more intense female display in the summer results from changes in female submissiveness and site fedelity. During the spring, shifts in territorial position may be accommodated because almost all areas have low food levels. However, the summer encounter proceeds with greater vigor because neither animal is willing to withdraw. The variance in food values between locations increases in July so areas now differ in their desirability. After several months in an area, each animal may feel established. During the fall, female-female encounters are interrupted by courting males.

Spatial exclusion between females is apparently not energetically practical. Although density dropped during the year, the mean overlap between females only declined

slightly during the year, suggesting that females clump. The lower frequency of attacks in female intrasexual encounters would make non-overlapping territories unlikely. When females disappear, other females in more peripheral, inferior areas may move into the better areas now vacated and maintain high levels of overlap.

Identifying the cues by which females chose good territorial sites proved difficult. Only tentative conclusions can be made. The sexual differences in shifting of activity centers suggest that females select a site only once a year (in May) and perhaps only twice a lifetime. Because the choice in May is generally not altered later, such an important decision should be based on predictable cues related to the long-term value of the area.

The extent of rocky substrate correlated significantly with female density. This result reflects the need for good basking sites among gravid females in May. Although the number of crevices was less important in explaining female distribution, it was clear that rocky areas which were devoid of crevices were avoided. The proximity of crevices is probably quite important but the actual number available is not the critical factor. Gravid females in May and early June are especially awkward in their movements at a time when they must bask frequently. Crevices close by would provide retreats from predators.

The importance of food distribution was not conclusively established. Females may be strongly influenced by the food distribution in early May, which was not measured in this

study. However, I doubt food values during a single month would be more important than the resources over the entire period from May to October. Gravid females may not fully utilize the food resources of their area until after parturition. Females dissected in May and early June (Chapter IV) rarely had large amounts of food in their stomachs prior to parturition compared to afterward (unpublished data).

There may be some predictability in the distribution of good food areas. How lizards recognize this predictability is not clear. Females that could recognize good areas would have higher survival or future fecundity. The presence of a large female, who presumably survived at that location and has returned, may be a good indicator of a desirable area, but the use of other individuals as cues for good sites is not clearly supported by the data. The frequency with which females overlapped males in May seemed lower than expected, considering the large relative size of male territories. The extensive territorial overlap between females, and clumping in their distribution despite the female-female aggression, suggests that attractive forces between females do not cause the overlap between females. Moreover, second-year females appear to use different cues than older adults. These younger females show less overlap with other females than did older females.

A surprising result was the tendency for second-year females to choose a new territory site in May, whereas older adults rarely did so. The stronger site fidelity among older females suggests that the decision to locate a

territory may be made only twice. Reluctance to move to a new location may correlate with the low probability of finding a better site. If differences between territories are small or a good site difficult to recognize, the risk of moving through unfamiliar terrain in search of a better location may outweigh any gain from the move. The risk would be highest in saturated environments. Some synergistic assessment of substrate, crevice availability and food may produce the observed female distribution.

The stable female territory sizes were not expected because food levels fluctuated during the year. Simon (1975) found an inverse correlation in S. jarrovi between food abundance and territory size in all age-sex classes except adult females. In her study, both sexes reduced territory sizes when additional food was placed in the territory. If these observations applied generally, reductions in territory size accompanying increased food levels in the summer should be expected but were not observed. The difference between Simon's study on the importance of food and this one may result from procedural differences in measuring territory size, particularly the time interval used (two days in Simon's study versus 30 days) and the pattern of food levels in each study area. Simon did not report the sharp change in food levels from June to July that were found in my study. The relatively small adult sizes reported by Simon (1973), compared to reported sizes for other populations (Goldberg, 1971; Ballinger, 1973; this study) might also result in

different spatial patterns and behavioral interactions between individuals.

A food hypothesis for the function of territories leaves unexplained sexual differences in territory size unless variation in foraging patterns, item size preferences or energetic requirements can be demonstrated. The smaller size of female territories in S. jarrovi is consistent with a sedentary tendency of females observed in other species (Irwin, 1965; Turner, Jennrich and Weintraub, 1969; Judd, 1975). Exceptions occur when the females lay eggs outside their territory (Blair, 1960). Sedentary habits in females, particularly in the breeding season, would allow greater partitioning of energy into gametes than would active habits.

Male behavioral patterns were strikingly different from females and correlated strongly with the fall breeding season. Most North American lizards have life cycles involving spring or early summer breeding (Fitch, 1940; Blair, 1960; Tinkle, 1967; Berry, 1974). The fall breeding season in S. jarrovi (Goldberg, 1971) has selected for different behavioral strategies in male competition for females. Unlike most species in which males perform certain breeding activities including territorial establishment first (Howard, 1920; Woodbury and Woodbury, 1945; Spoecker, 1967; Immelman, 1971; Christiansen, 1971; Burkholder and Tanner, 1974), male S. jarrovi establish their territories between May and July after the females have settled. Final locations of male territories are not determined until August. Consequently,

this difference reduces the advantage of high aggression levels between males in the spring as may be found in spring breeding lizards.

Males showed increasing aggressiveness through the months of activity (May-October). Tolerance between males was lowest in the fall, as indicated by the frequent male-male interactions, the increased "minimum distance" and the reduced territorial overlap. Coinciding with the increases in aggression were more conspicuous display behavior (i.e., frequency of sightings), greater daily movement and often larger territories. High aggression in lower density situations has been previously reported in Uta stansburians (Tinkle, 1967), Sceloporus merriami (Milstead, 1970) and S. undulatus (Vinegar, 1975a). Vinegar hypothesized that if males in high density situations spent more time fighting than those at low density, they would suffer a higher risk of injury and spend less time gathering food or courting females. Both factors would contribute to a loss of reproductive success among highly aggressive individuals and favor those with lower aggression levels. This argument seems applicable to S. jarrovi.

Several avenues of evidence suggest that the most critical resource for a male is females. The increases in aggression and territory size with the approach of the breeding season are devices for controlling access to females. A male S. jarrovi with strong territorial defense in the spring may expose himself to predators such that his chances of survival to the fall are greatly reduced. Selection

would then favor those individuals having lesser aggressive tendencies in the spring. As the breeding season nears, the chances of successful mating improve and the benefit from aggressive defense will increase, favoring higher levels of aggression in the fall. The point at which gain exceeded risk would be the optimum time for territorial establishment, and this time may vary between individuals. Large males or those returning to a previously used location may defend their areas effectively in the spring through advantages of size or site familiarity. Conspicuous display, which attracts predators, should be avoided. The scramble for areas would be most intense in aggressiveness when a resident disappears as the stakes (potential gain) have increased. Scrambles in late July or August should be more intense than those earlier in the summer as the likelihood of breeding has improved.

Males seek to maximize the position of their territory relative to the distribution of females. The greater shifting of male activity centers results from their efforts to arrange their territory over the maximum number of defendable females. The centering action serves to reduce the defense effort by minimizing the perimeter that must be patrolled.

Patterns of male territory size do not relate in any simple fashion to other behavioral patterns. Increases in male territory size should result from increased aggression combined with greater daily movement. Territories expanded in July and August, correlating with increasing aggression

but before activity (distance moved) showed substantial change. This suggests movement may be underestimated during the summer, if there is a direct relationship between territory size and movement. Some of the increased territory size results from reduced boundary pressures as animals are lost through predation or competitive exclusion. The diminished overlap of male breeding territories indicates that the entire monthly area has been converted into a carefully guarded territory. Although territories prior to September may not meet some definitions of territoriality (see Pitelka, 1959; Schoener, 1968) because of undefended border areas and submissive behavior by some males, during the breeding season the classical model of territory is more nearly approached. Consequently, the amount of space vigorously defended actually increases more dramatically than represented by the data on territory size alone (Figure 7). This sharper increase in defended area between August and September is consistent with the sharp increase in movement during the same period.

Resource priority goes to the largest male in a given area. However, smaller males have opportunities to take over a territory if larger males disappear, because male survivorship from May to September is fairly low (30-40%, unpublished data) and because which individuals will disappear is unpredictable. This potential favors the male who remains in or near the dominant's territory by being submissive when finding a good alternative site is risky. Occassional successful breeding by young males may be the

selective advantage of hierarchical behavior.

The inverse relationship between male density and male territory size results from each individual competing for the largest possible area containing females. Male possession of a large area allows exclusive access to the females there and eliminates potential interruptions during courtship (see Chapter III). The persistent skewness favoring females in sex ratios of second year animals indicates that males of this age class are pushed out of the study area by larger and usually older males. Second year males also display more submissive behavior than older ones. Apparently, submission does not always prevent exclusion. Yearling males are also under attack by older males. However, exclusion is less successful because yearlings are less conspicuous.

Some predictions about the relationship between ecological factors and aggression levels in lizards can be made. Testing such hypotheses will require knowledge of both survivorship patterns and mating systems of species. Three aspects will be considered: longevity of adults, the length of the breeding season, and the pattern of food distribution. Annual species with only one breeding season per lifetime (semelparity) should have high aggression levels as the competition for females will be very severe. Species which have substantial longevity should have lower aggression levels than semelparous species. High aggression has been included among those factors which are considered to

represent high reproductive effort (Williams, 1966) but the causal relationship between aggression and survivorship patterns is unknown. Whether the high population turnover of the semelparous species is a result of competitive or extrinsic factors may be important in the evolution of aggressive behavior. Different demographic regimes may result from these factors (Wilbur, Tinkle and Collins, 1974).

The duration of the breeding season should also select for a particular optimal aggression level. If the breeding season is extremely short, defense of space may waste time (a critical resource). Species with prolonged or year-round breeding should maintain a constant, perhaps lower, level of aggression than species with short and highly seasonal breeding seasons. Where breeding is prolonged over time, intense fighting over females may be disadvantageous as other breeding opportunities will occur over short periods of days or weeks, during which time animals have high expectancies of survival. Injuries from escalated fighting would tend to lower survival. In the absence of immediate reproductive benefit, avoidance of injury may be important. Shorter breeding seasons (several weeks) favor highly aggressive individuals during the actual period of mating, but outside the breeding season, high aggression is energetically wasteful and probably reduces survival.

The impact of food resources upon aggression levels is unclear, as food levels have not been carefully measured in populations showing different social systems. As food

levels increase, so should density. When males are in close proximity, aggressive behavior may risk injury and detract from mating and feeding. Hierarchical behavior is then possible. Hunsaker and Burrage (1969) discussed hierarchical structures in lizards but did not consider the means by which high density would persist in evolutionary time or occur frequently enough for selection to act. Two-rank situations between animals with overlapping home ranges may be the most common hierarchical pattern, although more complex social structures will occur (Evans, 1951). Demonstrations of natural hierarchies in the absence of localized food sources supporting temporarily high densities of lizards are necessary to support a hypothesis that hierarchical behavior is adaptive to animals of all ranks.

A model in which territory and hierarchy represent end-points of a behavioral continuum has been suggested by various investigators (Davis, 1958; Willis, 1967). More recently, Campanella and Wolf (1974) suggested a three factor continuum, adding individual distance. However, these models do not explain all observed variations in social behavior among lizards. The skink Leiolopisma zelandica is reported to be non-aggressive (Barwick, 1959) and Cnemidophorus species are highly aggressive but non-territorial (Christiansen, 1971). Stamps (1973), Berry (1974) and this study reported elements of territorial and hierarchical behavior within single populations. While populations with mixed strategies may represent those groups which are intermediate along the territory-hierarchy

continuum, the similarity of social structures in these three species may not result from the same selective forces.

Demonstrations of seasonal behavioral patterns can be useful in identifying critical resources for animals. In S. jarrovi, the reduced seasonal variation of females contrasts with the striking changes in male behavior. Patterns observed can be best interpreted as indicating females are the limiting resource to males. On the other hand, females behave in a way that suggests the choice of a good territorial site is a critical factor. Females may use several environmental factors in their "decision". Whatever factor influences female distribution, females are somewhat clumped, which enables males to defend areas containing several females.

CHAPTER III

BREEDING BIOLOGY OF SCELOPORUS JARROVI

Differential reproductive success among organisms is the driving force in evolution. The means by which an organism obtains mates and invests in its offspring have evolved to maximize the parent's genetic contribution to future generations. Consequently, a behavioral strategy which enhances mating success is subject to strong positive selection. The strategy most successful would depend upon the temporal and spatial distribution of the opposite sex.

Male strategies must solve the problems of temporal and spatial unpredictability of females. Even if females can be located with some precision, they must be receptive to courtship. Males may defend mating or ovipositing sites as a means of controlling access to females. Besides locating females, a male must display his fitness during courtship to promote female readiness to mate.

The wider variance in male reproductive success predicted by current models of mating systems (Orians, 1969) has been reported in a wide variety of organisms (see review in Trivers, 1972). However, phenotypic correlations of male RS have not been demonstrated in a systematic fashion for any species. This insufficiency prompted the present portion of this thesis, using the lizard Sceloporus jarrovi.

Polygyny is the predicted breeding system in lizards because they generally give no parental care after

egg-laying or parturition. While monogamy in lizards has been reported, no explanation of the selective value for monogamy among lizards has been satisfactory (Tinkle, 1967). As part of a long-term study on the behavior of S. jarrovi, I attempted to quantify the degree of polygyny occuring in this species and to relate differences in reproductive success with measurable phenotypic attributes of males. Such information would provide insight into the relationship between behavioral patterns and strategies that maximize reproductive fitness.

In order to make a relevant interpretation of breeding behavior, I attempted to answer the following specific questions: 1) What is the mating pattern? 2) How do males control access to females? 3) What environmental factors influence the variance in male RS? 4) How extensive is the polygyny? 5) What phenotypes correlate with male RS? and 6) How does hierarchical behavior enhance RS for submissive animals?

METHODS

The breeding structure of Sceloporus jarrovi was determined by intensive field observations of courting males during the 1972-74 breeding seasons. Displays and courtships (interactions including a shudder approach) were recorded as they were observed in the field. All residents were marked (see Introduction), so pair associations and the frequency of courtship between pairs could be determined. Sex ratios and age structures of breeding populations were also determined for each year. I computed the mean body size of each age class by sex in order to assess the degree of sexual dimorphism in size, if any, which occurred in the population.

For analytic purposes, the breeding season was arbitrarily defined as a period of 18 observation days for each year, which encompassed all adult matings observed plus three to five days preceding the first mating and one to three days following the last. This standardization of the length of the breeding season eliminated differences in territory size or activity between years resulting from the varying time intervals over which mating activity was observed.

Based on observations of courtships and matings, I made two estimates of male reproductive success (RS). The first method (the "known" estimate) assigned only those females to a particular male when (1) mating of the pair

was observed, or (2) the female's territory was overlapped exclusively by that male during the breeding period. This estimate was considered highly reliable because observations indicated females mated only once and exclusive overlap indicated a low probability that the female met another male. The second method (the "probable" estimate) attempted to assign all mature females to mature males. The females not assigned in the "known" estimate were then credited to males by the following criteria:

(1) more than one male overlapped the female's territory but only one male was observed courting the female.

(2) more than one male was seen courting the female but one courted much more frequently than the others.

(3) yearling females were assigned to yearling males when possible.

Preferential assignment of yearling females to yearling males was made on the basis of (1) yearling avoidance of older adults, (2) observations that yearlings breed after adults complete their breeding, and (3) avoidance of biasing the offspring assignments in favor of larger and older males. Assigning yearling females to either yearling males or older males did not produce statistically significant differences in results during preliminary analysis of correlations between phenotypic traits (see below) and male reproductive success. Consequently, I believe use of the

last criterion above does not affect the interpretation of the results.

Following these assignments of females to particular males, I determined the number of females with which each male mated and the number of potential offspring, based on fecundity estimates of the females (Ballinger, 1973), assignable to each male. Mortality of gravid females and their young subsequent to the breeding season was ignored in the assignment.

The estimates of reproductive success (RS) made according to the two methods explained above were then tested for significant relationships with several phenotypic characters of each male, as follows:

1) body size: the snout-vent length of the male.
2) age: estimates in years judged from growth records and body size.
3) activity levels: the number of days the male was sighted during the breeding season (as narrowly defined).
4) territory size: the area encompassing all sightings of the male during the breeding period and corrected for sample size bias (see Chapter II for procedures).
5) aggression: the percent of all spring staged encounters with a particular male resident that reached level 4 (defined in Chapter II) and also the percent of level 4 encounters during staged situations in the fall.

6) movement: the average meters/hour an animal moved during observations of breeding activities.

7) duration of domicile: the number of months previous to the breeding season (not exceeding four) that the territory holder lived in the area, even if not the dominant.

8) courtships: the number of courtships seen performed by a particular male during the breeding period.

Phenotypes of males judged successful by the "known" estimate were tested (t-test) against those of all other males. A similar analysis was performed based on offspring assignments of the "probable" estimate.

Since the RS data were heteroscadastic, a log transformation was made. Transformations using square root or square functions were no more successful in reducing heteroscadasity than log functions. I avoided negative log values by adding one to the RS of each male before transforming data. This dummy variable did not affect the distribution of points. Stepwise regression analysis was performed to determine which factors were most significant in each breeding season. Simple linear regressions for each phenotypic character were performed for each breeding season. Parameters were tested for normality by plotting regression residuals. Because of the discontinuous nature of reproductive success, assumptions of normality were

generally violated using all data points. Covariance analysis of regressions indicated neither slope or intercept differences in any regression between years for a particular trait. Data for all years were combined to test a linear model of the relationship between phenotypic characters and male RS. Regression analysis was also performed on all males, exclusive of those with zero RS, to characterize the pattern of success within this group. This subgroup met assumptions of normality for most phenotypic variables.

RESULTS

The Breeding Season

Adult males began persistent shudder displays at females in late August. Previously, such displays were short and ended at the slightest indication of female disinterest. Adult courtships were observed from late August until late October. The number of courtships observed during this period increased daily reaching a peak coinciding with observed matings. I observed twelve copulations and two near-copulations (tail under but no insertion) between adults from September 20 until October 13, 1972-74. The yearly range in the dates of mating observations was most narrow in 1973 (seven days) and widest in 1974 (17 days).

Courtship by yearlings was concentrated in October, but extended into November in some years. Two matings between yearlings were observed: October 30, 1972 and November 11, 1973. The later breeding activity among aggregated yearlings in 1973 coincided with delayed parturition (see Chapter IV) and prolonged fall growth in that year, allowing some individuals to reach mature size, and to breed, very late in the fall. The observed asynchronous breeding of yearlings and adults was an important factor in the decision to assign yearling females to yearling males in the estimates of male RS.

Courtship Patterns

I observed 242 instances of males displaying at females during September and October. Of these, 141 (58%) included a shudder display, a display which brought the male within several centimeters of the female. Courtship was initiated by the male, but in a few cases, a female's bob seemed to encourage the continuation of courtship by a male who had stopped displaying.

A typical courtship occurred in the following manner: Upon sighting a female, the male ran to within a meter of her. A male initially performs pushups (displays are described in Chapter II), or stationary shudder bobs, followed by nearly continuous shuddering while the male approached the female. Receptive females were almost completely passive toward the male and lay flat on the ground. Females might bob or shift position during the early stages of courtship. The male continued his shudder bobs and partially circled the passive female. Sometimes the male licked the female one or several times on the flank, but licking was usually omitted (seven of 11 cases). When the female had remained still for several moments, the male suddenly bit the female on the neck and climbed on top of her. While holding her, the male might bob or drag the female 180°. The pair might not move at all. The male then laid quietly on top of the female, heavily panting for about fifteen seconds, before forcing his tail under the female's tail, bringing his cloaca against hers. In only

one of the 14 matings did the female thwart the male's first attempt to place his tail under hers. Intromission lasted for three to five seconds with no motions. The pair then separated when the female moved from under the male. The male might bob or shudder-bob at the female upon separation. This prompted the female to show signs of possible rejection, such as tail waving or moving away.

If the female was not receptive, she would repeatedly move away from the courting male. One rejection posture involved the female's turning her back to the male, holding her tail at a stiff but characteristic angle (about 45^{o}) from the body axis and moving away from the male while seemingly dragging her cloacal region on the substrate. Among females already mated or seen late in the breeding season, the female would wave her tail in the courting male's face. The waving became more frantic if the male approached or persisted in his displays. The "sidlehopping" display reported for other Sceloporus (Carpenter, 1962; Vinegar, 1972) was never observed.

Sequences of displays and responses are used by lizards to identify species and sex of other individuals (Hunsaker, 1962; Ferguson, 1966). The passive response by females in this species and in other iguanid lizards seems to serve as a releaser for male courtship. No male was observed to bite and mount a female that was not completely passive. All but one mounting were eventually successful (i.e., the female raised her tail or allowed it to be raised). The

submissive female posture may override other cues identifying the sex of the intruder. A tethered male who was completely passive was courted and mounted by two male residents who attempted copulation.

Age Structure and Sex Ratios of Breeding Populations

Variations in age structure and/or sex ratio could strongly affect the pattern of reproductive success among individuals. Fitness is relative to the population in which an organism competes. A second year animal will have greater success in a population where it is relatively large in size than in a population where it is dominated by older animals. Similarly, the intensity of the male-male competition may be reflected in the degree of skewness in the sex ratio.

The age structure varied between the three breeding seasons studied (see Table 10). Among males, two-year-olds dominated the population of 1972 and 1974 but there were many older males in 1973 surviving from the previous year. In 1972, two-year-olds were disproportionately successful (Figure 20). In other years, three-year-olds showed a disporportionate success. The importance of age in predicting male RS will be examined later.

Sex ratios also varied between years (Table 10). In 1972 and 1974, sex ratios heavily favored females (0.52 and 0.74 M/F, respectively). In 1973, the sex ratio was close to unity and slightly in favor of males (1.16 M/F). As already seen, regardless of the sex ratio, males differ

TABLE 10

THE AGE STRUCTURE AND SEX RATIOS OF BREEDING POPULATIONS OF SCELOPORUS JARROVI 1972-74.

Age Class	1972		1973		1974	
	M	F	M	F	M	F
Immature	4	4	3	19	2	8
Yearlings	5	7	9	6	5	2
Second Year	5	11	3	2	10	20
Third Year	1	7	5	7	2	1
Fourth Year	2	-	3	4	2	3
Fifth Year	-	-	2	-	1	1
Total Mature	13	25	22	19	20	27
Mature M/F	0.52		1.16		0.74	
Population Total	17	29	25	38	22	35

in their RS. However, in 1973, the variance in RS among males was reduced. This may result from the near unity sex ratio or from a more uniform distribution of females throughout the study area in that breeding season.

Sexual Dimorphism

One correlation frequently observed between the morphology of an animal and its breeding system is the relationship between the extent of sexual dimorphism and the degree of polygyny (Darwin, 1871; Selander, 1958, 1965, 1972; Orians, 1969). This relationship is postulated to result from female choice of bigger males. Recently other factors have been suggested which may influence the degree of sexual dimorphism (Moreau, 1960; Schoener, 1967; Selander, 1972). Because factors such as different feeding preferences between sexes may select for differential body sizes, it is important to demonstrate not only the degree of dimorphism in a population but that the larger body size of the male, but not the female, is adaptive toward mating success.

When the body size of all individuals in the breeding populations of this study is computed by known age class, males are larger than females in their first fall (t-test, $p<.01$) and at each age thereafter (Table 11). In fact, the magnitude of the differences increases with age, from 8% to 11% of the average male size for each age class.

Dimorphism in color also occurs. Like some other Sceloporus, S. jarrovi have blue throats and lateral belly

TABLE 11

DEGREE OF SEXUAL DIMORPHISM

BY AGE CLASS IN SCELOPORUS JARROVI

Age	Male Size Mean ± S.E.	Female Size Mean ± S.E.	Difference Means	T-Test	Sig.
1	55.52±3.37mm	51.08±3.43mm	4.44mm	5.34	p<.001
2	78.35±3.98	70.15±3.79	8.20	7.16	p<.001
3	86.87±3.76	78.48±3.33	8.39	5.51	p<.001
4+	90.90±2.64	81.12±1.46	9.78	9.37	p<.001

markings. Females are light to medium blue in these areas and show no seasonal changes in color. Some males were indistinguishable in blue color from females prior to July. However, in July, males develop deeper, metallic-blue colors that contrast sharply with the paler colors of females. Yearling males first displayed adult colors in late August as they reached 54mm snout-vent length. Only one subadult (53mm) among 37 yearling males captured in 1974 had adult throat colors. Very old males showed areas of melanic pigment near and in their throat and belly patches.

General body color also differed between the sexes and age classes. Females, regardless of age, and yearling males had predominant brown dorsa, broken by patternless black or white markings. Males in their second summer began developing a black colored dorsum, with white scale tips. The contrast between black and white became more brillant during the fall. Older males also showed tints of turquoise on the head and tail which increased in intensity during the fall.

Male Breeding Strategy

Previously (Chapter II), I demonstrated that certain male behaviors changed as the breeding season approached. Female behavior did not change or did so in directions differently from the male pattern. Males increased their activities significantly during the breeding season. This increase, both in daily activity and distance moved, produced more conspicuous and effective defense of the territory. Greater territory sizes and reduced overlap

between territories resulted. Males with several females in their territories appeared to search for these females. Many long(>10m) movements were observed without any visible stimulus,and moves up to 30m were recorded if a female was sighted.

Two behavior patterns appear designed to assure exclusive access to females: 1) monitoring the female's receptivity by daily courtship and 2) centering the territory around as many females as possible while minimizing the perimeter to be defended.

The high level of male activity in the fall seems adaptive in locating females when they first become receptive. Assuming that coition inhibits receptivity (Crews, 1973), a male who mated with a female soon after she became receptive would enhance his chances of excluding other males from mating with that female. If the female became unreceptive within hours after mating, the female would likely reject any other male that she encountered. If rejection could occur within minutes, as suggested by work on Anolis carolinensis (Crews, 1973), the male would be assured of the paternity of the offspring. The best strategy for a male, considering the pattern of female receptivity, is daily courtship of females. This pattern was particularly obvious among those males with several females.

A second method of assuring females is creation of an exclusive area. The location of the territory may be its

most important characteristic. A traditional explanation for territoriality as an area free from interference during courtship (Howard, 1920; Nice, 1941) is supported by observations of four encounters where one male interrupted another male's courtship. Two of the four cases involved a bigger male stopping a courtship by a smaller male. In the third, the males were the same size. In the fourth case, the smaller male did not disturb the bigger male until it had mounted the female. At this point, with the bigger male biting the female on the neck, the smaller male attacked the bigger male and effectively stopped the mounting.

The delay between territorial establishment (spring or summer) and the fall breeding season in S. jarrovi means males must compete over a long period of time, defending an area with the most females possible but the smallest perimeter. Changes in aggression level and size of male territories during the year suggest males do not defend their areas vigorously until some chance of breeding develops. Predation reduces the number of neighbors and some animals move. Only 30-40% of the spring males survive to September. A slightly higher (50%) survival rate occurs in females. Consequently, one would expect that important areas in the spring may not correlate with areas most desirable in the fall due to the loss of females. The tendency for males to shift their territories more during the year than females (Figure 10) may result from the

efforts of males to maximize the value of their area by shifting or incorporating areas with females. To test this hypothesis, two vectors were determined. One (the observed change) was the direction of change in the male's activity center from May to the breeding season. The other (predicted direction) was the vector that would be expected if the male moved his May activity center toward the two nearest females which were still surviving in September. The difference in direction between the two vectors was measured (Figure 18). The direction of the observed shift in activity center of males (N=21) is clearly not random (χ^2 test, $p<.01$).

The Breeding Structure

Male S. jarrovi are polygynous. Whether the "known" or the "probable" estimate is used, males had varying degrees of reproductive success (Figure 19). Three of the nine adult males observed to mate did so with two or three females. When all females are assigned to a male on some basis, male success ranged from zero to eight females. The variation in RS expressed in numbers of offspring produced is shown in Figure 19. Of the offspring assigned in the "probable" estimate, 77% were assigned by matings or exclusive overlap between male and female territories (Table 12). Examination of the distribution of offspring by age class of the adult male indicated breeding was dominated by two-year-olds in 1972, by older males in 1973 and weakly dominated by older males in 1974 (Figure 20).

Figure 18. Directionality in shifts of male activity centers from May to the breeding season (September 15 - October 15). The figure shows the number of individuals whose observed shift deviated from a predicted shift toward the nearest two females by values less than some multiple of 30 degrees.

Figure 18

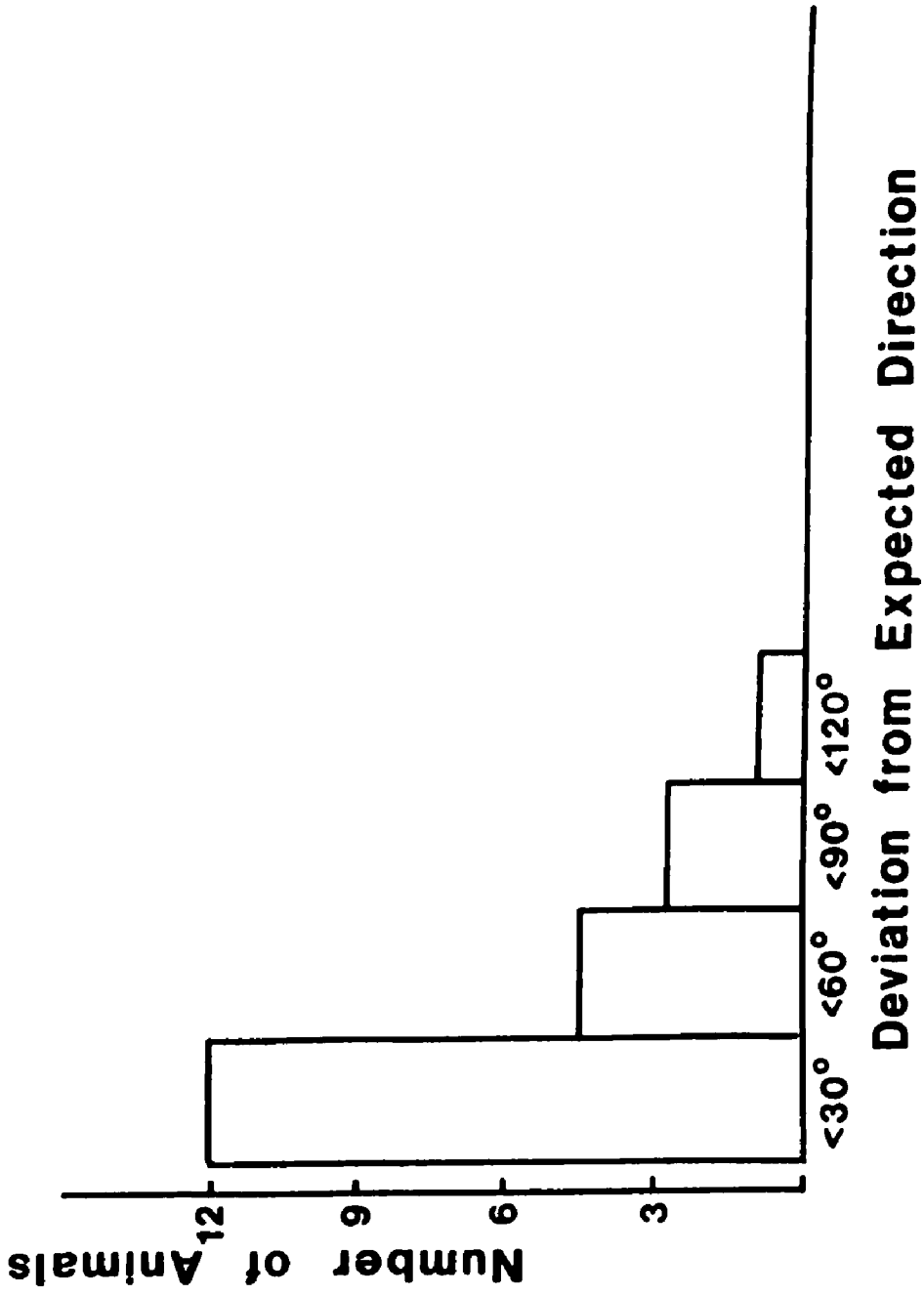

Deviation from Expected Direction
<30°
<60°
<90°
<120°
Number of Animals
12
9
6
3

Figure 19. Differential reproductive success in Sceloporus jarrovi. The "known" histogram represents those males whose success was determined by observations of matings or exclusive overlap of territories. The "probable" histogram represents all males using several criteria. Females are shown in the second histogram for comparison.

Figure 19

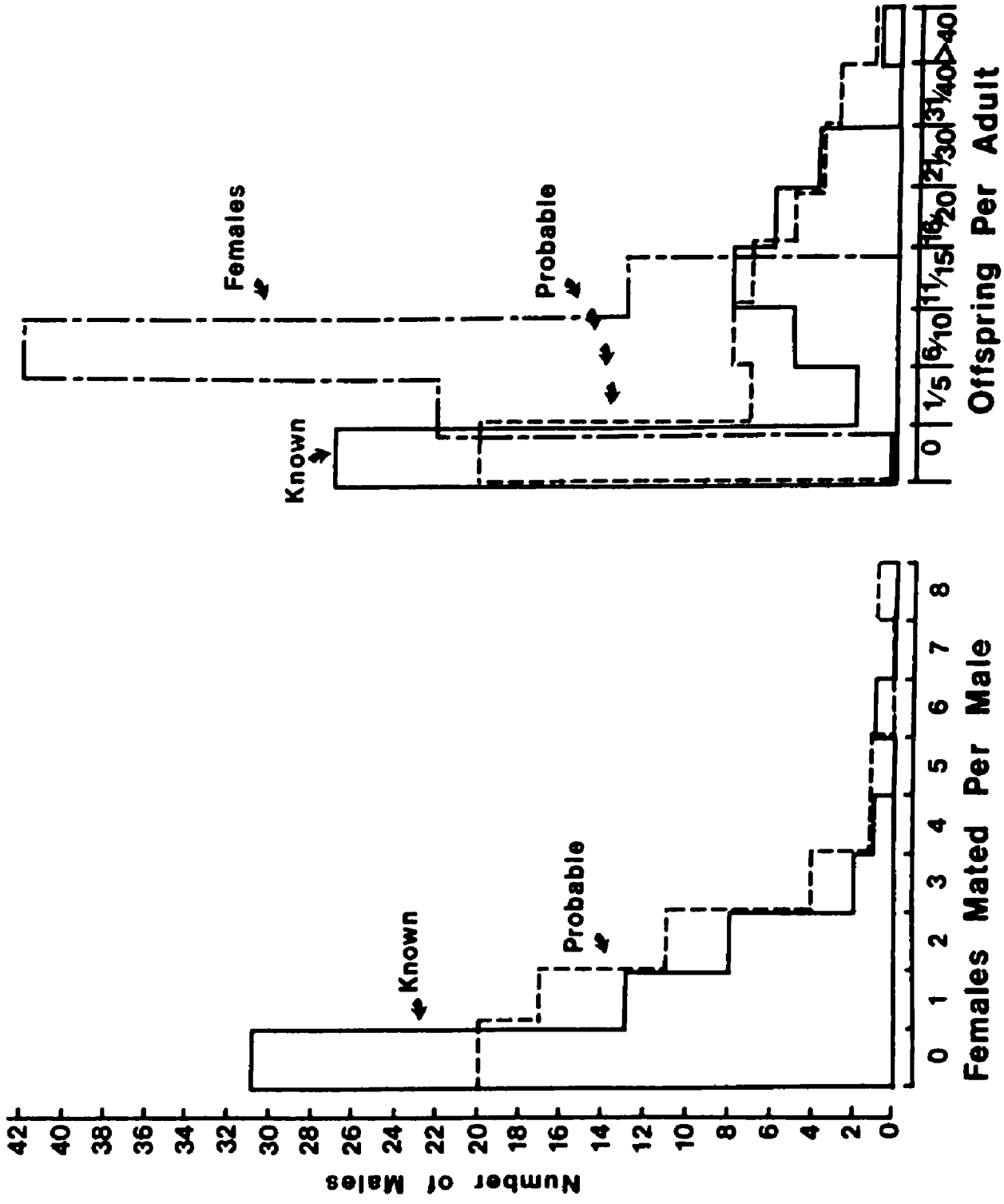

Females
Probable
Known
0
1/5
6/10
11/15
16/20
21/30
31/40
>40
Offspring Per Adult
Known
Probable
0 1 2 3 4 5 6 7 8
Females Mated Per Male
42 40 38 36 34 32 30 28 26 24 22 20 18 16 14 12 10 8 6 4 2 0
Number of Males

TABLE 12

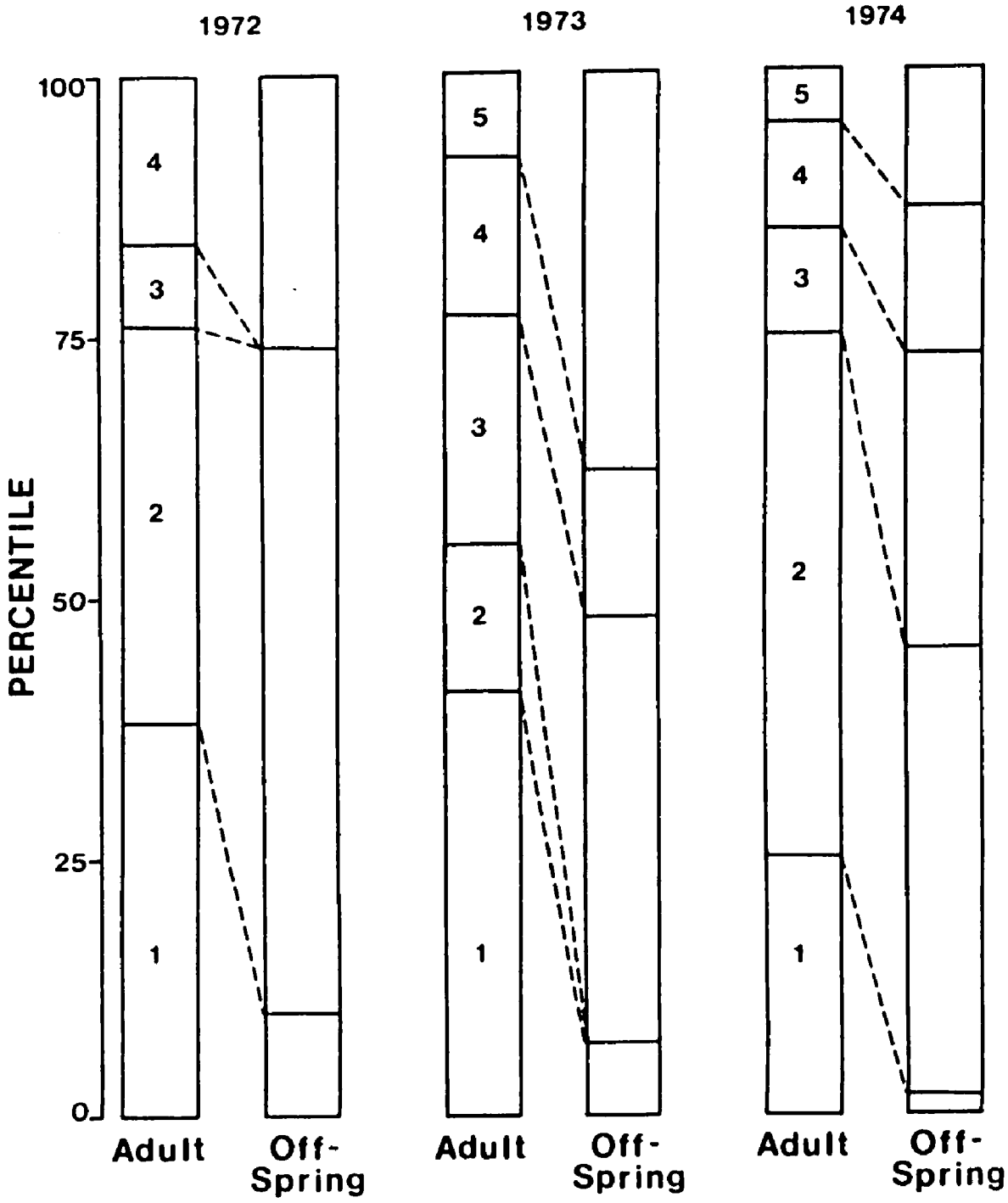
THE IMPORTANCE OF THE VARIOUS CRITERIA USED FOR ASSIGNING OFFSPRING TO MATURE MALES ("PROBABLE" ESTIMATE)

Criterion	Number of Offspring	Percent Total
Observed Mating	116	23
Exclusive Overlap of Territories	280	54
Only One Male Courted	44	9
The Most Frequently Courting Male	43	9
Yearlings (remaining)	32	6

N = 515

Figure 20. The proportion of each age class in the male breeding population and the potential offspring attributable to each age class. Numbers identify the age class of the adult males.

Figure 20


1972
1973
1974
100
75
50
25
0
PERCENTILE
5
4
3
2
1
Adult
Off-
Spring

Even though the overall sex ratio was near unity in 1973, breeding was still polygynous. The greatest variation in male RS occurred in 1972, when the sex ratio was heavily biased toward females.

Fifteen of the 67 females (22.5%) seen courted were involved in courtships with two or more males. Nine of 15 (60%) were seen in courtship with a second male only once. Four females were courted by three males and two were courted by four males. In each case, one male was the dominant resident; the others were subordinates in the same territory or residents in a neighboring territory. In addition, eight of 12 females actually seen copulating did so with the male that courted most frequently.

The duration of time that females are receptive is important in assigning offspring with confidence. Observations on females before and after mating permit a high degree of confidence in assigning females to the male with whom they mated. All six of the females seen the day before mating were observed to reject a courting male and one of the females rejected a male on the morning of the day on which mating occurred. All five females seen on the day after copulation rejected a courting male. Since all 14 females observed in mating were later seen in their territories, the absences of some females on the day after mating do not represent captures by predators or emigration. Absences after copulation would assure sufficient time for inhibitions against mating to develop if inhibition

was not immediate. Successful mating did not prevent a male from courting a female with which he previously mated. Fifteen such courtships were seen. One pair was seen in courtship four times during several days after a successful mating.

Rejection after copulation did not always occur. One female apparently mated twice with the same male, seven days apart. Another female allowed courtship to proceed to the neckbite before resisting the male, with whom she had mated several days earlier. In addition, tethered females could be mated with several males over two or three days before they showed signs of rejection. The artificiality of tethered encounters, however, requires that they be interpreted with caution.

I assigned most yearling females to yearling males, although this may overestimate the success of that age class. Evidence suggested that yearlings(by definition, sexually mature) rarely mated with older adults. Most yearling courtships were observed in October, by which time most older adults had already mated. Only two, brief courtships of adult females by yearling males were observed. Tethered encounters indicated no physical barriers existed to such matings. Similarly, yearling females always ran from courting adult males. The courting activity among aggregated yearlings in 1973 suggests that in some years yearlings may breed substantially later than adults, as

noted above. Adults rarely even bob at each other while aggregated, so I believe adults do not mate at this time.

Phenotypic Correlates of Male RS

The relationship between male RS, as measured by the two methods described above, and behavioral and phenotypic attributes of males was investigated by statistical analysis. While correlation and regression analysis cannot prove a causal relationship between the variables tested, comparison of statistical results with empirical observations may suggest testable hypotheses suitable for future investigations.

A correlation matrix of male phenotypes with the "known" estimate is shown in Table 13 . Eight correlations are significant, more than expected by chance alone. Reproductive success is significantly ($p<.05$) correlated with SVL, activity and the number of observed courtships. Since courtship did not enter into the assignment procedure for estimating RS, the correlation of RS with courtships is particularly interesting. Despite the strong correlation between SVL and age, age is not correlated with RS in males. I believe this result is an artifact of the data subset and not a true phenomena. The "known" estimate includes few yearlings, whose lower RS contributes heavily to the overall correlation between age and RS (see Figure 22). The number of months of residency approached significance with RS ($p<.09$) and was weakly correlated with activity ($p<0.1$). Surprisingly, territory size and aggressiveness

TABLE 13

THE CORRELATION MATRIX BETWEEN PHENOTYPIC ATTRIBUTES OF MATURE MALES AND THE "KNOWN" ESTIMATES OF RS.

BS(SVL)	1.0							
Age	.7938**	1.0						
Act	.6940**	.4397*	1.0					
Ter	.1570	-.1744	.2621	1.0				
Court	.2220	.0410	.4845**	.2090	1.0			
Agg	-.012	-.2446	.3062	.1887	.2599	1.0		
Months	.2008	.0864	.2947	.2558	.4847**	.3331	1.0	
Offsp	.3903*	.0564	.5843**	.3260	.7355**	.2504	.3682	1.0
	BS(SVL)	Age	Act	Ter	Court	Agg	Months	Offsp

* = p .05

** = p .01

do not correlate with the "known" estimate of RS. Data on movement and fall aggression scores proved unsuitable for analysis, and were omitted.

The attributes of males known to have mated (those in the "known" estimate) were compared with those for which mating success was unknown. The mean value of phenotypic characters for each group is shown in Table 14. Males known to have mated were significantly (t-test, $p<.01$) larger, older, and more active. Frequency of courtship was nearly significantly ($p=.11$) different between groups. The same attributes were identified as significant when the analysis was repeated using the "probable" estimate.

The statistical correlation between the "known" estimate, which does not use courtship frequency to assign females to males, and courtship increases my confidence in the "probable" estimate which uses courtship to assign $\approx 18\%$ of the total offspring. Observations on the 14 females actually seen mating support the association between mating and high frequency of courtship. Eleven of the 14 females would have been assigned to the male with which copulation occurred if courtship frequency was the criterion. The remaining thre would have been assigned to the "correct" male on the basis of exclusive overlap between female and male territories.

The correlation analysis was repeated for the "probable" estimate (Table 15). Parameters of significance in the previous analysis remain so. Male age and months of domicile are now significantly ($p<.01$) correlated with male RS. The

TABLE 14

THE PHENOTYPES OF MALES WITH KNOWN BREEDING SUCCESS

VERSUS THOSE OF MALES WITH UNKNOWN SUCCESS

PARENTHETICAL VALUES ARE SAMPLE SIZES

Attribute	Known Mated (Mean ± 1 S.D.)		Unknown Mated (Mean ± 1 S.D.)		t-test	Sig.
SVL (mm)	83.73±10.59	(26)	65.38±11.22	(29)	6.216	p<.001
Age (years)	3.077±1.23	(26)	1.52±0.78	(29)	5.664	p<.001
Activity (days)	13.23±4.62	(26)	7.55±4.41	(29)	4.658	p<.001
Territory (m^2)	681.04±577.67	(26)	692.79±522.21	(29)	.079	p>.5
Months	2.68±1.21	(22)	2.22±1.30	(9)	.939	p>.25
Courtship	3.00±4.68	(26)	0.60±0.699	(10)	1.600	p>.1
Aggression	31.62±32.87	(16)	21.66±20.20	(3)	.500	p>.5

TABLE 15

THE CORRELATION MATRIX BETWEEN BEHAVIORAL ATTRIBUTES

OF MATURE MALES AND THE "PROBABLE" ESTIMATES OF MALE RS.

SVL	1.0							
Age	.87**	1.0						
Act	.60**	.53**	1.0					
Ter	.05	.08	.11	1.0				
Court	.22	.041	.48	.209	1.0			
Agg	-.01	.244	.306	.188	.259	1.0		
Months	.20	.086	.29	.25	.48	.333	1.0	
Offsp	.57**	.47**	.63**	.19	.78**	.1525	.40**	1.0
	SVL	Age	Act	Ter	Court	Agg	Months	Offsp

* = p .05

** = p .01

similarities in the two correlation matrices strengthen my confidence in the "probable" estimate. The two estimates are highly correlated because 77% of the offspring were assigned by the conservative criteria (matings or exclusive overlap of territories).

Stepwise regression analysis was performed to identify the most significant factors in determining male RS. Using six phenotypic characters (SVL, age, activity, territory size, courtship frequency, and months of residency), activity was selected as the most important predictor of RS in 1972 ($p<.05$) and in 1974 ($p<.01$). In 1973, SVL was the most important variable ($p<.001$). When significance levels for inclusion into the regression equation were relaxed, no variable was added to the regression in 1972, three were added to the 1973 regression and only one variable (months of residency) was added in 1974.

When only four variables (SVL, age, activity and territory size) are considered in a stepwise regression analysis (because these four variables were known for all 55 males), different variables were selected in each year. Activity remained significant ($p<.01$) in 1972 but age was selected in 1973 ($p<.01$) and SVL was chosen in 1974 ($p<.01$). However, when all three years were considered together, SVL was chosen as the most significant variable ($p<.001$). Excluding SVL as a variable, the analysis was repeated. Age was substituted for SVL in the 1974 regression ($p<.01$). For the regression representing all three years together,

both age and activity were included in the regression ($p<.001$).

When phenotypic characters are considered independently, regression analysis can be used to test whether phenotypes correlated with male RS in a linear (additive) fashion. Data were analyzed by year and for all three years combined. Analysis of covariance indicated regression of variables for different years were not statistically different in either slope or intercept ($p<.05$). Assumptions of normality are violated in most parameters because of the discontinuous distribution of male RS. Variables are more normally distributed when males with zero RS are excluded from analysis.

Body size (SVL) was a good predictor of male RS in 1973 and in 1974 ($p<.001$). The variance explained by the variable was 50-53% in each year. SVL was not significantly correlated with male RS in 1972 ($p>0.1$). For all three years combined (Figure 21), SVL was highly correlated with male RS ($p<.001$). The combined data gave a R^2 value of .40. A regression using all data exclusive of those males with zero RS was also significant ($p<.001$).

The age of breeding individuals, which correlates significantly ($p<.01$) with SVL in this species, also correlated significantly with male RS in 1973 ($p<.001$) and in 1974 ($p<.01$). Age explained 60% of the variance in 1973 but only 38% in 1974. Age was also highly significant ($p<.001$) for all years combined (Figure 22) but the R^2 value

Figure 21. The influence of snout-vent length (in millimeters) upon the log of male reproductive success. The solid line is a least squares regression. The slope of the line is highly significant ($F=36.32$, $p<.001$).

Figure 21

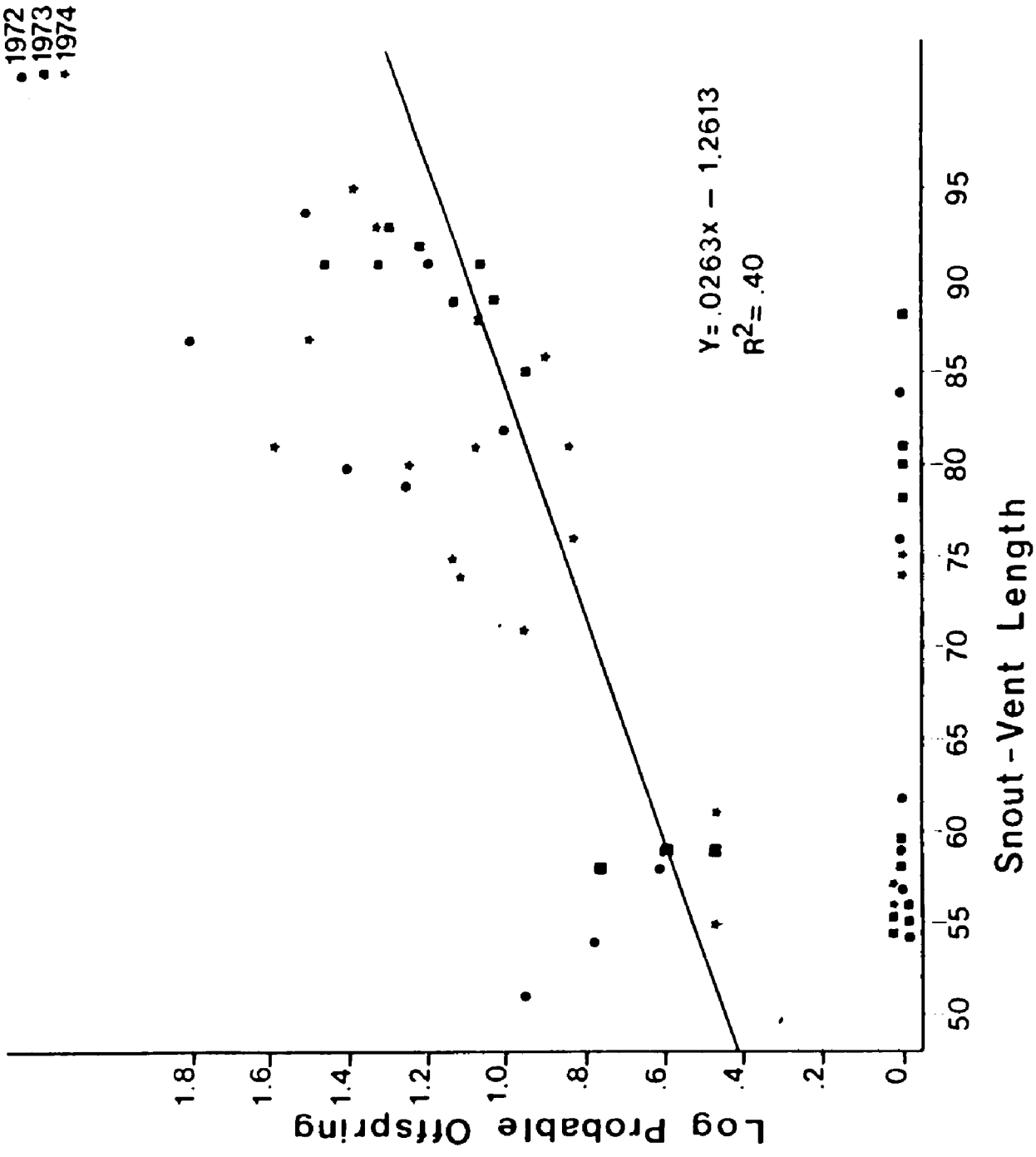
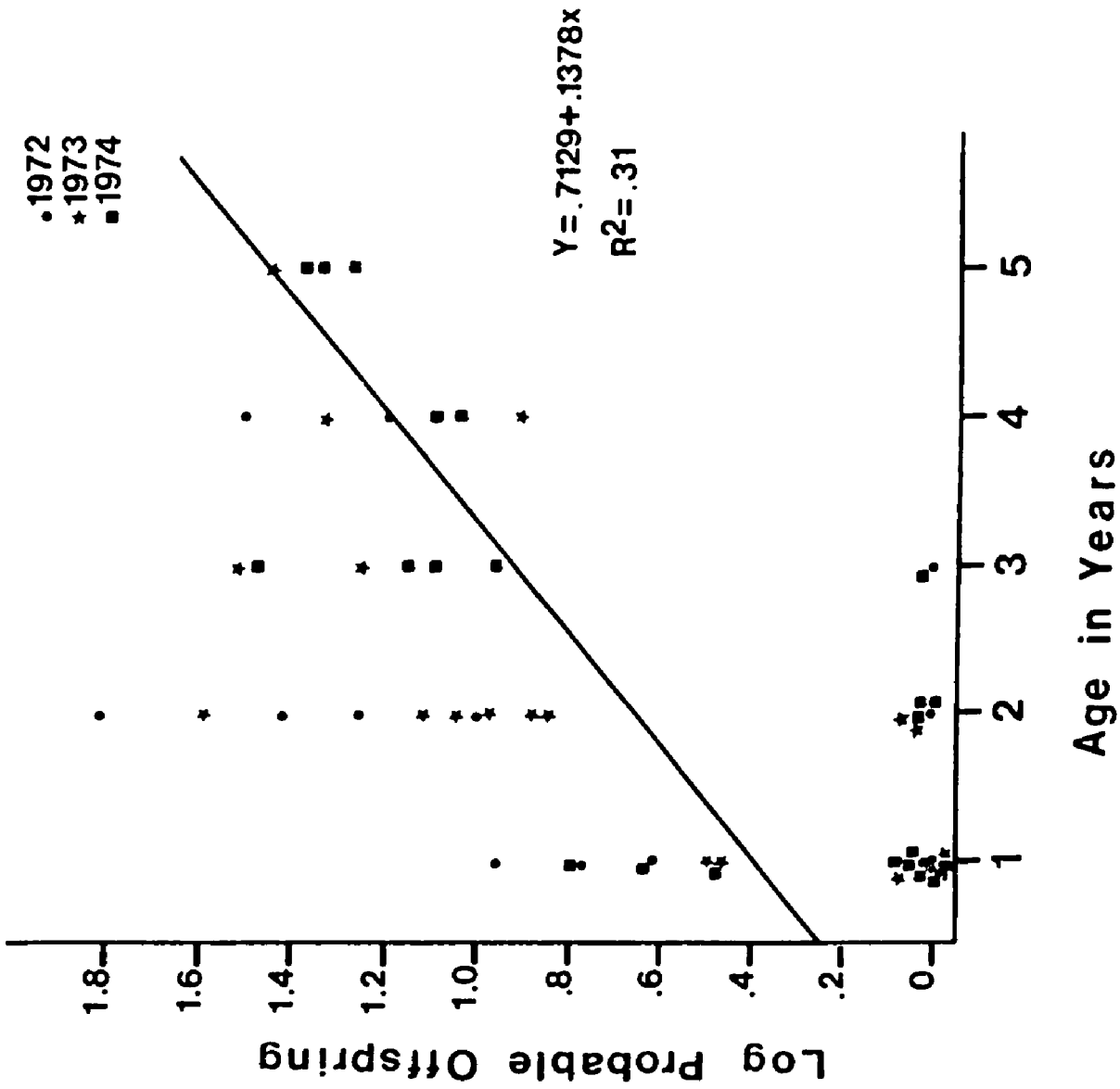

1972
1973
1974
Y=.0263x − 1.2613
R^2=.40
Log Probable Offspring
Snout-Vent Length
0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
50
55
60
65
70
75
80
85
90
95

Figure 22. The influence of age upon the log of male reproductive success. The solid line is the least squares regression. The slope of the regression is significant ($F=31.57$, $p<.001$).

Figure 22


•1972
*1973
■1974
Y=.7129+.1378x
R2=.31
Log Probable Offspring
Age in Years
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
0
1
2
3
4
5

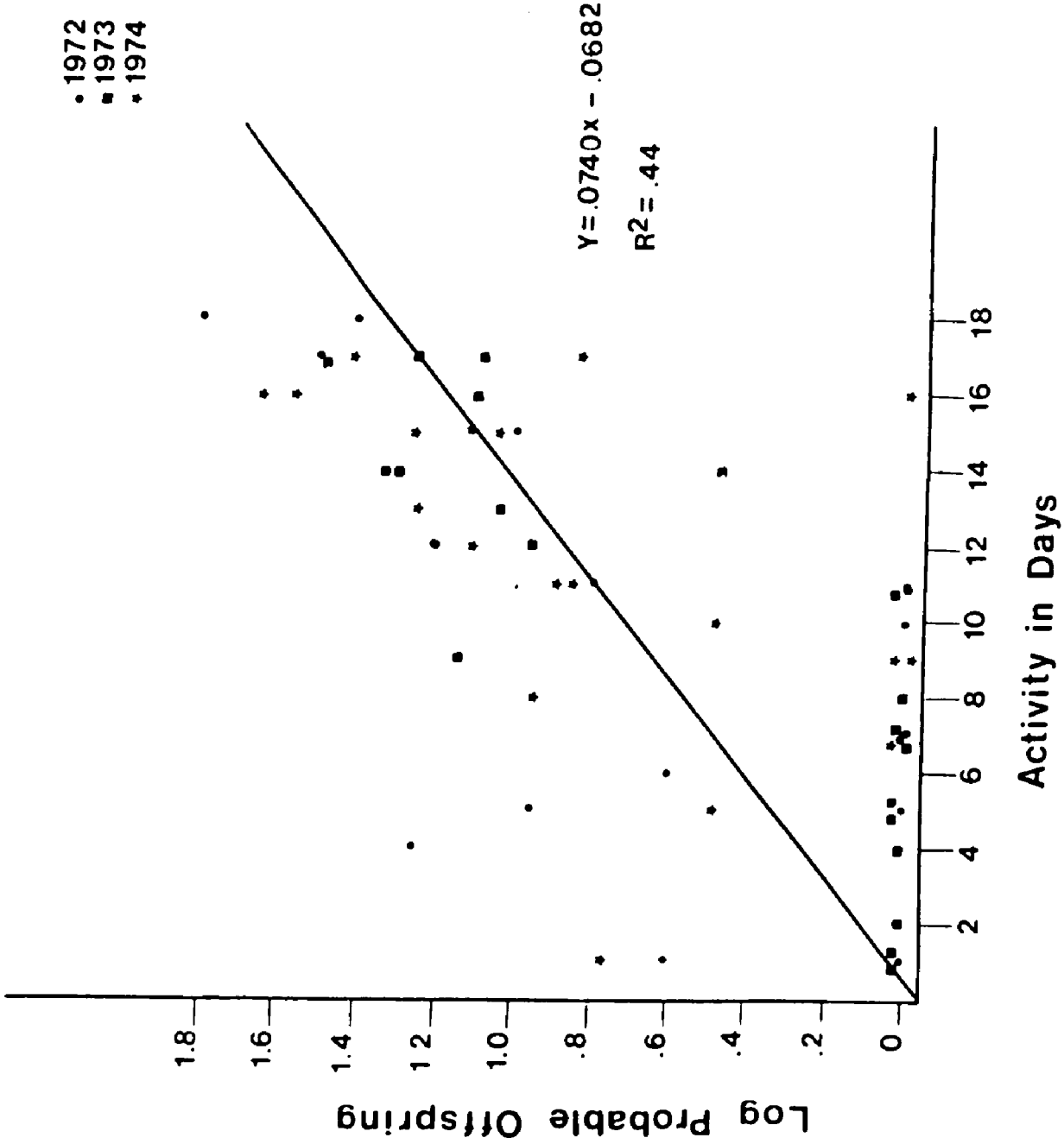
was .37. The lower significance of age as a predictor of RS suggests females may distinguish between small and large members of an age class, particularly among second year animals which have the widest variance in size. Comparison of RS between second year males above and below 80 mm SVL (the range midpoint) did not support this hypothesis (Mann-Whitney U test, $p>0.1$).

Activity, the number of days an individual was sighted during the breeding period, varied widely among animals. Regressions with male RS were highly significantly ($p<.01$) for each year. The variance explained by the variable ranged from 35 to 47%, depending upon the year. The significant ($p<.001$) regression using all data (Figure 23) has a R^2 value of .44. It appears that a high level of visibility on one's territory is necessary for acquiring females. Dominant males or males secure on their territories (known mated column, Table 14) would have high levels of activity. Yearlings and subordinate second year males would be less predictable in their habits and less visible to observers. If they increased their level of activity, they would risk attacks by the dominant. Courtships by subordinates would also be susceptible to interruption. However, activity is also significantly correlated ($p<.01$) among males with positive RS, indicating the value of the parameter is not solely derived from the contrast between dominant and subordinate males.

Measures of aggression were consistently poor

Figure 23: Influence of daily activity upon the log of male reproductive success. The slope of the least squares regression is highly significant ($F=42.71$, $p<.001$).

Figure 23

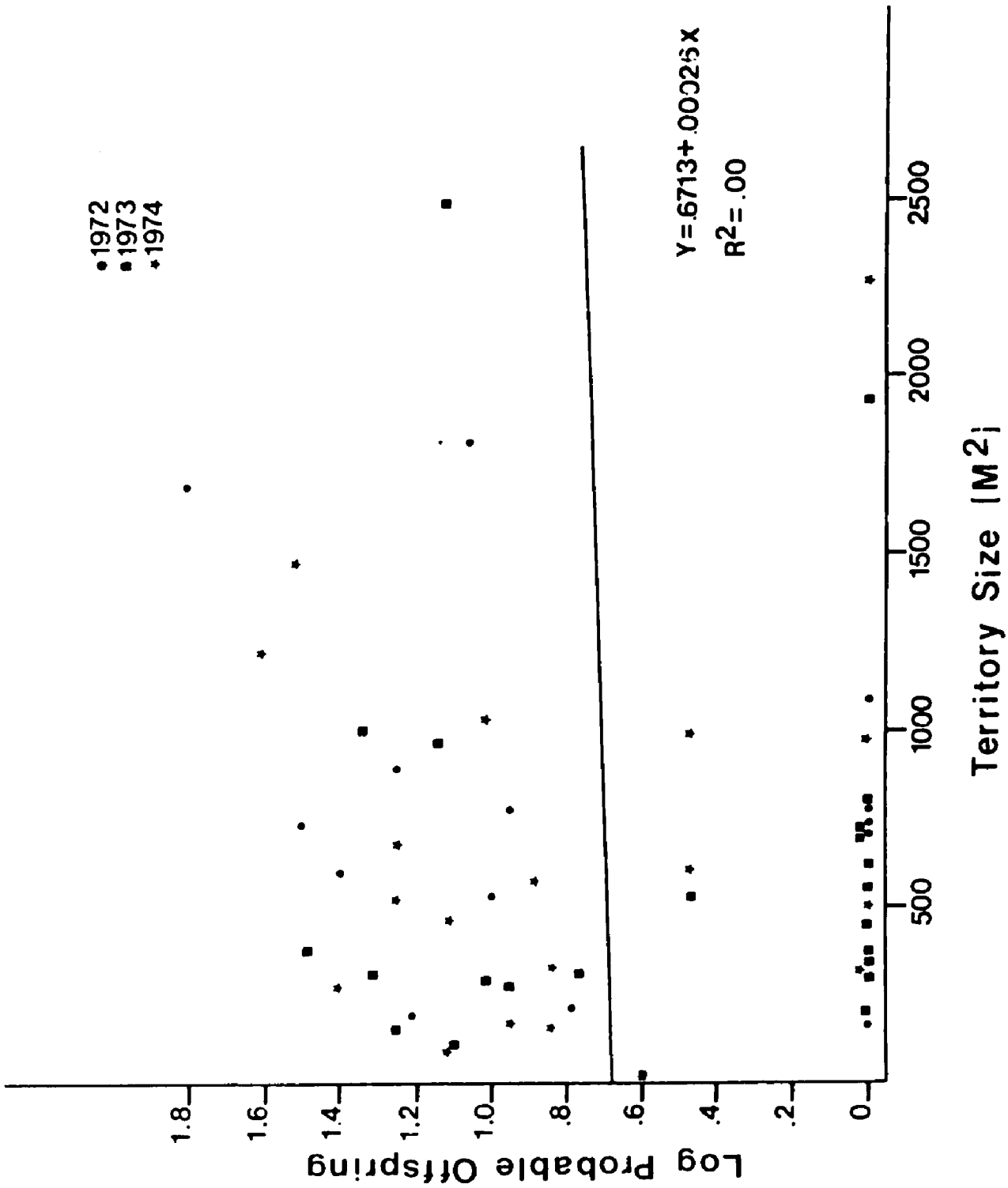

1972
1973
1974
Y=.0740x - .0682
R2=.44
Log Probable Offspring
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
0
2
4
6
8
10
12
14
16
18
Activity in Days

predictors of male RS. Fall staged encounters were uniformly high in rank (see Chapter II) and did not differentiate individuals. I tested whether animals still present in September were significantly more aggressive in the spring than those not surviving to September. The scores for tethered encounters of animals in these two groups were not significantly different in aggression level (Mann-Whitney U test, $p>0.1$). Among the group not surviving to September are individuals captured by predators and those who lost aggressive encounters and left the area. The analysis would be more meaningful if the predation losses could be eliminated. In addition, encounter scores grade the displays given but do not include all the factors that may determine the outcome of natural interactions. Body size (Figure 4) strongly influences the outcome of encounters. Several large (90 + mm) individuals with high breeding success had low or inconsistent scores in staged encounters. Their size may give them an advantage in encounters which reduced the intensity of the observed displays.

Territory size might be a good predictor of male RS, as larger territories should overlap more females. In no year, however, was territory size significantly correlated with male RS (Figure 24). In 1973, some of the smaller territories were held by adults with the highest RS. This pattern coincided with very restricted activity by females in the fall of 1973, resulting from unseasonably hot weather. Although much of the scatter in territory size results

Figure 24: The influence of territory size upon the log of male reproductive success. The slope of the regression is not significant ($F=.03$, $p>0.5$).

Figure 24


•1972
▪1973
*1974
Y=.6713+.00025X
R2=.00
Log Probable Offspring
Territory Size (M2)
0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
500
1000
1500
2000
2500

from the large and poorly defended territories of first year males and subordinate males, territory size remained insignificant even when males with zero RS were excluded from the analysis.

Courtship frequency was significantly correlated with RS in each year. However, it is impossible to determine whether this is a real correlation or the result of observer bias. The number of months an adult male occupied its breeding territory during the year was correlated with male RS only in 1974 ($p<.01$). When data from all three years are combined (Figure 25), the regression was non-significant. The male who returns to a previously used area in the spring or settles early in the spring and maintains his position until the breeding season may have some reproductive advantages. Data presented elsewhere indicates this strategy may have certain liabilities also, particularly due to the loss of females during the year.

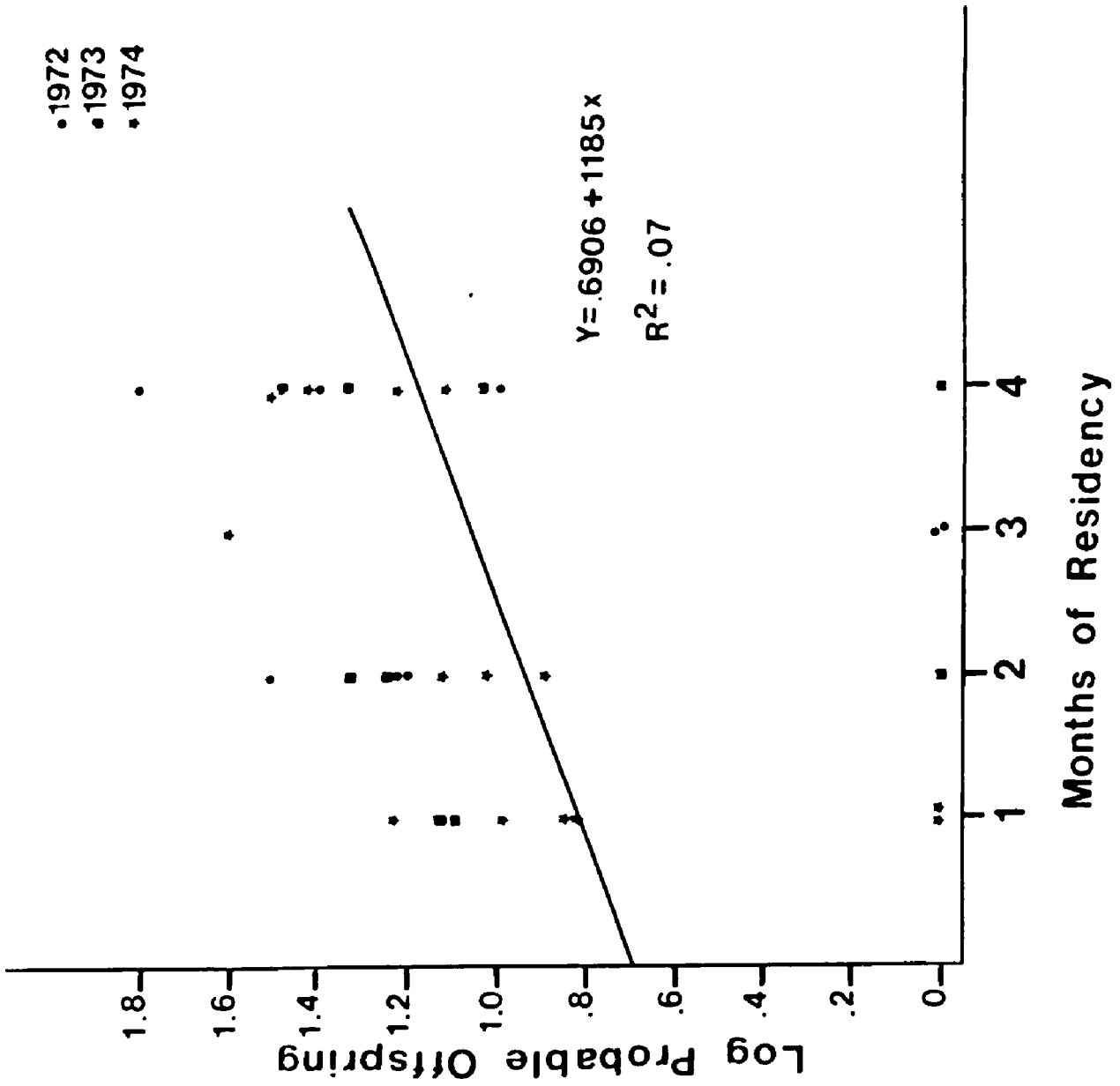
Male reproductive success is heavily dependent upon the size of the individual and various attributes which are correlated with size (age, activity). While territory size was not correlated with male RS, possession of a territory was essential for any chance of breeding success. Animals not holding an exclusive or largely exclusive territory would likely have zero RS.

Adaptiveness of Hierarchical Behavior

Previously, evidence of hierarchical behavior among males was presented (Chapter II). While wide overlaps

Figure 25: The influence of duration of domicile upon the log of male reproductive success. The slope of the regression is not significant ($F=2.29$, $p>0.1$).

Figure 25


•1972
•1973
•1974
Y=.6906+1185x
R^2=.07
Log Probable Offspring
Months of Residency
0
.2
.4
.6
.8
1.0
1.2
1.4
1.6
1.8
1
2
3
4

between territories occurred during the spring and summer, most overlaps were reduced or eliminated by September. During the three breeding seasons observed, nine two-year-olds maintained a territory that broadly overlapped the territory of a larger male. Such extensive overlaps were associated with submissive behavior by the smaller male or careful avoidance of the larger male. In a sense, the nine with broadly overlapping territories represent the "unlucky losers" who failed to acquire an exclusive territory because the dominant survived. However, such individuals may have an advantage in the following year upon the disappearance of the dominant or a neighbor in gaining control over the area.

A crude measure of the success with which subordinates may breed was made. Thirty second year males had territories overlapping other males by 45% (an arbitrary figure) for at least one month during the year. Of these thirty, twelve survived to the breeding season and seven had some success in reproducing (always by replacing the missing resident). Of the twenty-seven males who did not overlap other males as broadly, and generally had isolated territories on the periphery, survival was lower (7/27) but the difference between the two groups is not significant (χ^2 test, $p>0.1$). Of the seven survivors in this non-overlapping group, four had some RS. The survivors in an overlapping situation might be more likely to have higher RS than survivors at a solitary site. However, the two

groups did not differ in RS (Mann-Whitney U test; $p>0.1$). The lack of differences can be attributed to high success by two males in the nonoverlapping category from 1972, a year in which all males had some RS due to the highly skewed sex ratios. It would appear that the success of of the subordinate strategy varies from year to year and may be highly unpredictable to the animal.

DISCUSSION

The breeding system of Sceloporus jarrovi is polygynous, with males promiscuously courting all females they encounter and females resisting most approaches. Similar breeding behavior has been reported with varying degrees of quantification in most lizards studied to date (Blair, 1960; Harris, 1964; Rand, 1967; Carpenter, 1967; Trivers, 1972; Berry, 1974). Coupled with these courting patterns in S. jarrovi are striking sexual differences in activity during the breeding season. Seasonal patterns of behavior appear coupled to sexual differences in critical resources (see Chapter II). Females pick an area in May probably for its food value while males postpone territory establishment until summer when they try to maximize the number of females within their area. Boundaries of male territories are finalized in late August just prior to the breeding season.

In S. jarrovi, a combination of female choice of area and of mate seems to occur. The female clearly picks an area in the spring for her territory at a time when the male present may be a poor indicator of the male who will be available in the breeding season. On the other hand, females also generally have opportunities to choose between two males. This is indicated by the 22% of females seen courted by more than one male, and by the female potentially shifting her home range to make a neighboring male available for comparison.

Males attempt to assure themselves access to females and thereby deny the female any choice by frequent courtship to detect receptivity and by increased defense of the territory to reduce overlap with other males. The presence of subordinates persisting into the fall indicates that the defense is not always successful in assuring exclusive access to the females. Males generally do not attempt to coerce a female to move into their area, although one case of such behavior may have been observed. In courtship the sexes have conflicting goals: the male seeks the maximum number of matings but the female can optimize her success by mating with the most fit male she can find. Males may then attempt to deceive females as to their fitness or rank on the territory. Consequently, females who discriminate against "deceivers" would be favored by natural selection. One way females may prevent deception is by limiting mating to the male who courts frequently, who is presumably the dominant ("most fit") male in the area. The dominant is also the largest male, whose ability to survive has been demonstrated by his size.

The temporally uncertain aspect of breeding is when the female will become receptive. Receptivity apparently starts suddenly and is inhibited by copulation, although the data on one undisturbed female and the tethered females prevent a conclusive answer. This receptivity pattern favors a male strategy of daily courtship of a female, in order to make the receptive period as short as possible and prevent the female from mating with other males. The

significance of courtship in predicting male RS was demonstrated in this study, indicating that the energy expenditure has been rewarded over time. Consequently, the male builds more fat reserves during the summer than he needs for winter survival along (Goldberg, 1971) in order to devote maximal time in the fall to mating activities and a minimal effort at feeding behavior.

The advantages of mating inhibition upon receptivity to the female is not clear. Crews (1975), in a study on Anolis carolinensis, suggested vulnerability to predators while mating favored inhibition by minimizing the time spent in copulation. However, S. jarrovi breed during a period when predator pressures are relatively low (as suggested by high survival rates in the fall). The risk of exposure to a predator may be low, but the benefits of remaining receptive and finding a second male are dubious. Inhibition may prevent injury from additional neckbites in subsequent courtships by the same or a different male. Rejection signals may shorten the time the female is courted when she is not receptive, allowing her to commit more time to food gathering. If a female could identify a good male and mate with him, there would be little selection against ovulation or other internal events following mating. The hormonal state would be altered and receptivity ended.

The inhibition of receptivity after mating is part of female choice. Behavioral patterns, interacting with

hormones, may result in females showing distinct preference for one male over another. The actual evidence for choice in S. jarrovi is weak; the clear preference for one male over another was not observed. Less than 25% of the females in this study were courted by more than one male. Several cases were observed where the female rejected a male the day before or after mating with a different male. Rejection because hormonal conditions were not right and rejection because the male was less desirable should be distinguished. Determining the reason for female rejection of a courting male may prove very difficult.

The two estimates of male RS allow quantitative answers to the question of what attributes enhance the individual male's contribution to the next generation. The general agreement between the two estimates as to which traits are statistically important strengthens the value of the more complete "probable" estimate which assigns all females. The importance of body size (SVL) toward RS is not surprising, as it has been found to be important in other studies (Trivers, 1972, discusses several). Despite a high correlation to SVL, age is much less useful in predicting RS. Because body size related to success in aggression encounters over spatial disputes (Chapter II), its relationship to RS is expected. Some of the predictability of the outcomes of encounters is lost by using age rather than body size. Despite the intuitive relationship between body size and aggression, the "aggression" estimates fail in the analysis because simple numerical

values are poor estimates of a behavior pattern that is modified by many factors. Besides the body size difference between combatants, the location of the encounter and past experience may influence observed agonistic behavior. Larger or older animals are likely to have been residents at a particular site longer and less likely to abandon an area during an encounter.

A second cluster of phenotypic characters also correlated with male RS. Activity, number of courtships and months of residency were correlated with RS and with each other but only activity correlated with body size. Activity is strongly influenced by the ability of the resident to defend his territory, display conspicuously and win encounters when he finds an intruder. The time spent courting is logically related to activity. However, it remains unclear why activity levels vary so widely among adults, if this parameter is useful to the male in obtaining females. The frequency of courtships by a male is a function of his fitness, rank on the territory and the number of females available. A male with only one female will not court the female endlessly when she is not receptive. However, a male with several females is likely to follow up an unsuccessful courtship with one female by searching for others. A female need not mate with the male who courts most frequently although it may be advantageous to her to do so.

Despite the intuitive connection of aggression and territorial behavior to breeding success, neither measure

was significantly correlated with male RS. In addition to the difficulties of measuring aggression by a single value, there are selective advantages in showing submissive behavior during the spring and summer among smaller males, in order to avoid injury and remain in a dominant's area. Since encounters prior to mid-July have little probability of assuring the area to either combatant, a viable strategy for some individuals would include submissive behavior to any larger male resident (and perhaps lesser aggression to an intruder). Since many individuals disappear during the summer, replacement by the submissive individual is possible with the subsequent potential increase in reproductive success. Such a submissive animal would then successfully defend the area from other individuals because he was familiar with it. Animals utilizing a submissive strategy would show low aggressive levels, thus precluding any correlation of aggression with RS.

The lack of relationship of territory size with RS would not be surprising if females were unequally dispersed and the quality of resources was variable, but important to the female, from site to site (Orians, 1969). Female territorial behavior is not strong enough in the fall to prevent clustering to a greater degree than in previous months. The consistent values of territorial overlap between females, despite declines in female density during the year, suggests female distribution is not random or even. Females may become more clumped in the fall as individuals move into good areas which are vacated during the summer as a result

of predator loss. This lack of evenness is exploitable by males in their attempts to include areas with the most females.

In addition to the irregular distribution of females, the lack of correspondence between male territory size and RS results from several other factors. Yearlings have large territories which they defend poorly. Some of the observed movement which generates the large areas may result from aggressive encounters with older males. Yearlings have little chance of high RS. Similarly, individuals without females in their area generally showed little site attachment and were rarely seen repeatedly in the same location, in contrast to the site fidelity of males with females in their area. Some peripheral males had long, shallow territories that bordered several males. These peripheral males searched for females in the absence of the larger neighbor. These searches appear to have low success rates, in terms of matings. It appears that two different male strategies with regard to the use of space may exist (Constantz, 1975). However, the reproductive advantages of the submissive strategy remain unclear.

CHAPTER IV

WINTER ACTIVITY AND THE ADVANTAGES OF VIVIPARITY

Many temperate zone lizards aggregate with the onset of winter (Worthington and Sabath, 1966), but only a few species are reported to be active while aggregated (Weintraub, 1968; Burns, 1970; Vitt, 1973). For those species where basking temperatures have been reported, winter basking raised body temperatures to near summer levels (Vitt, 1973; Tinkle and Hadley, 1973).

Winter basking may serve a variety of functions in different species. Sceloporus orcutti juveniles bask and feed while adults do not (Weintraub, 1968). Vitt (1973) found basking coincided with maximum speratogenesis in male Gerrhonotus coerulus and females apparently utilized basking periods to prepare ovarian eggs. Tinkle and Hadley (1973) suggested Sceloporus jarrovi females basked in order to enhance embryonic development and advance parturition dates. They could not identify the functional value of male basking, as breeding ended before the aggregations developed. As part of a long-term study on Sceloporus jarrovi in the Pinaleño Mountains in Arizona, I attempted to gather quantitative data on winter basking behavior in this species in order to answer three questions: 1) Since both sexes bask, are there sexual differences in the pattern of basking? 2) What are the advantages of winter basking for each sex? 3) Does winter basking indicate an inability to hibernate for the winter?

As part of a viviparous life cycle, winter basking may contribute significantly to the success of the individual. Like any adaptive strategy, viviparity confers certain benefits but with associated costs (Fitch, 1970). Certain correlates of viviparity in lizards, such as single-broodedness (Tinkle, Wilbur and Tilley, 1970) and apparently low predation pressure (because the clutch is lost if the gravid female is captured by a predator) suggest the habit can evolve only in long-lived species. However, the viviparous animal has eliminated losses from nesting and can control the developmental rate of the litter through behavioral means. It is this latter advantage of developmental control that may be exploited by winter basking (Tinkle and Hadley, 1973). Because of this array of advantages and disadvantages, and the greater proportions of species in montane and cold environments that are viviparous (Fitch, 1970), viviparity has been viewed as an adaptive response to these environments. Considering the phylogenetic diversity of viviparity in reptiles, the habit appears relatively easily evolved. The possibility that viviparity is irreversible (Fitch, 1970) cannot be determined from our present knowledge of the relationships between species.

Alternatively, winter basking may reflect an inability to hibernate successfully for extended periods. If hibernating animals emerged in the spring in a less viable condition than winter basking animals, winter activity would be favored. However, winter activity requires considerable

energy expenditure during the winter months compared to hibernation. Since Sceloporus jarrovi have rather low fat body reserves by March or April which may be insufficient for some individuals to survive the remainder of the winter (Goldberg, 1971), the high level of metabolism associated with winter basking may produce some risks. If these risks are real and not outweighed by compensatory benefits, one would expect age or sex classes which do not benefit by winter activity to hibernate rather than bask.

METHODS

Possible advantages and disadvantages of winter basking were investigated by field observations of aggregated animals and by laboratory manipulations. Field observations were made in late October through early December in 1973 and 1974. The main area of observation was a large rock-cut adjacent to the summer site, as described in Chapter I. Three hundred and fifteen animals were marked at this site. Of these, 255 were each seen at least three times during the six week period of observation in each year and thus considered residents.

A census of basking animals was taken daily, weather permitting, at early emergence and again at 1100 hours MST. Daily frequency of observation was determined for individuals in each age-sex class. Animals seen on eight selected days with two or more censuses were segregated into those seen only once and those seen in more than one census ("repeaters") in a given day. This procedure allowed detection of the proportion of animals basking longer than the 45 to 60 minutes necessary for a single census. The frequency of "repeaters" was expressed as a percentage of the total number of individuals in that particular age-sex class seen for all eight days. Daily frequency and repeater proportions were tested statistically for differences between age-sex classes and between years.

The date of parturition, defined as the date when 50% of a sample of ten adult females were postpartum, was determined for each year in two elevational ranges, < 1825m and > 2285m. Samples of females were collected 1972-74 at roughly ten day intervals in May and June until 50% were postpartum. No high elevation females were collected in 1974. Gravid females were dissected and the size, sex and number of embryos noted. Weather records were obtained from the weather station at Safford, Arizona (885m elevation), and the degree-days (sum of the daily maximum temperatures) calculated for two periods: the length of the aggregation season (November through April) and the entire gestation period arbitrarily started November 1.

The ability of gravid females to hibernate was tested in the laboratory. A sample of 94 gravid females collected in the Pinaleño Mountains at elevations from 1670m to 2190m was divided into four roughly equal groups: two groups were maintained at a constant 9° C. in a temperature control chamber and the other groups in a fluctuating regime of 9° C. at night and 26-28° C. between 0900 and 1600 hours. One of the warm groups was fed mealworms and the other group not fed in order to assess the effect of food on survival. All groups had access to water. The experiment ran from November 15 until March 15 when mortality reached 50% in one group. Animals were weighed at the beginning of the experiment and monthly during its run. Animals which died during the experiment were weighed and dissected to determine

fat body size and embryonic state. Six survivors in each group were sacrificed to determine fat body weights and embryo development at the conclusion of the experiment. Data from both cold groups were combined in the analyses.

In December 1974, I collected eleven gravid females in the Pinaleños (5 from 1800m, 5 from 2100m and 1 from 2770m) and placed them in warm conditions (about 30-32° C.) with abundant water and food in the reptile greenhouse at the University of Michigan Botanical Gardens. In early March, each female was isolated and checked daily to determine the parturition date and the size of the litter.

RESULTS

Each year, between October 20 and November 10, animals began aggregating for the winter on south-facing rocky cliffs with deep crevices. The number per crevice ranged from three or four up to an observed maximum of 63 animals on an isolated boulder with two large, adjacent crevices. Most aggregation sites were too warm for summer occupancy. Many potential winter sites, which appeared suitable to the observer, were not used by aggregated animals, perhaps because animals seek out other individuals in selecting a suitable location. Males who were previously observed guarding their areas from one another were now basking side-by-side without interaction.

The animals at the rock-cut ("winter site") provided the bulk of the basking observations. Only a few summer site animals utilized this area despite its proximity and apparent desirability over locations within the summer study area. Since the winter site supported only a few individuals during the breeding season and the areas surrounding it had a very low density of lizards, most animals in the aggregations there must have moved substantial distances (over 200m) to reach it. Numbers within the aggregations stabilized within two weeks after the beginning of the migration. Most animals were consistently located at the same crevice during the six weeks observation period each

year, although some shifting between adjacent crevices occurred. Feeding behavior was rarely observed.

The "summer site" had only poor aggregating places, as indicated by the few individuals seen in the area after November 1. More animals were sighted in the summer site during November 1974 than November 1973, but the numbers were still only a small proportion of the fall population. Winter survival could be estimated by recaptures in the summer site during the following spring, assuming animals return to the summer site when aggregations break up. The data, given by sex and age class in Table 16, indicate a high survivorship. Yearlings appear to survive less well than adults.

Basking Behavior Patterns

Animals emerged over a wide range of times (0830-1100) and displayed a bimodal activity pattern with reduced numbers of individuals active around noon. Differences in wariness existed between age-sex classes, with adult males the most shy. Most animals remained within one-half meter of a crevice. Yearlings were the most common among early emergers and also ventured the farthest from the crevice on warm days.

There were no differences in daily basking frequency between the several age-sex classes in a given year (Table 17). Animals of different sizes also failed to show significant trends (Figure 26) in basking frequency. However, daily frequency was significantly different between

TABLE 16

WINTER SURVIVORSHIP IN SCELOPORUS JARROVI
BY SEX AND AGE CLASS FOR TWO YEARS

	1972-73		1973-74	
Adult Males	9/9	100%	10/10	100%
Adult Females	17/18	94%	8/10	80%
Yearling Males	11/13	84%	7/11	64%
Yearling Females	9/12	75%	21/15	84%
AMONG YEARLINGS ALONE:				
Immature Males	4/4	100%	3/4	75%
Mature Males	7/9	77%	5/7	71%
Immature Females	2/3	66%	16/19	84%
Mature Females	7/9	77%	5/6	83%

The demarcation between mature and immature animals is 54mm SVL for both sexes.

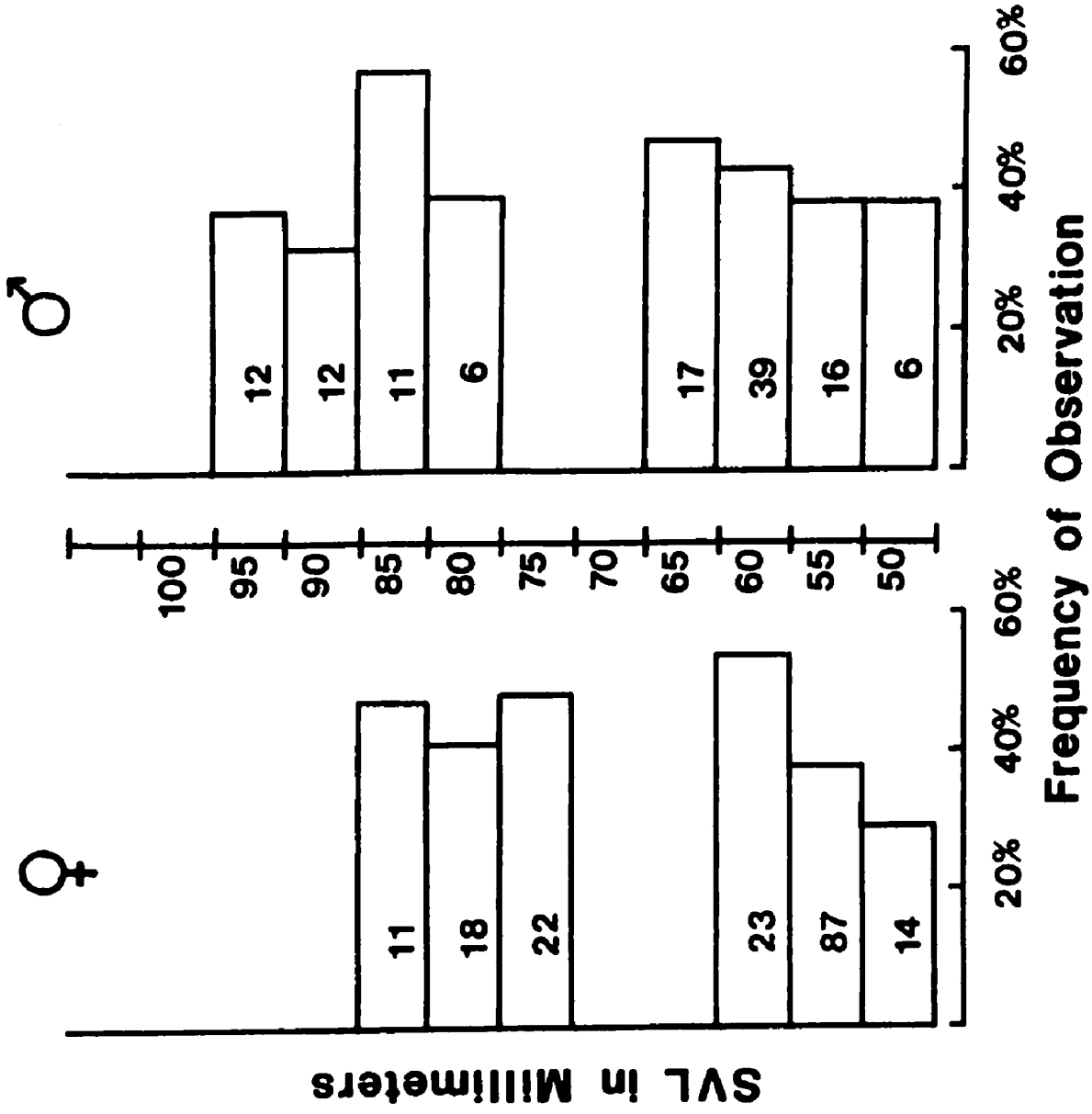
TABLE 17

WINTER BASKING PATTERNS: DAILY FREQUENCY OF OBSERVATIONS AND PROPORTION OF ANIMALS SEEN REPEATEDLY DURING ONE DAY. OBSERVATIONS ARE FROM A SIX WEEK PERIOD IN NOVEMBER AND DECEMBER 1973-74.

CLASS	DAILY FREQUENCY			PROPORTION OF REPEATERS	
	1973	1974	Sig		
Adult Males	29.5±10.87	45.5±17.18	<.001	22/81	27%
Adult Females	36.7±20.47	49.1±14.87	<.01	47/121	38%
Yearling	38.7±17.0	45.7±15.38	<.06	50/134	37%
Yearling	31.6±15.38	49.9±18.9	<.004	53/139	37%

Figure 26: The frequency of observation of basking animals by SVL intervals of 5 mm.

Figure 26


♂
12
12
11
6
17
39
16
6
100
95
90
85
80
75
70
65
60
55
50
♀
11
18
22
23
87
14
20%
40%
60%
Frequency of Observation
SVL in Millimeters

years for three of the four age-sex classes (t-test, $p<.01$) and nearly significant for the fourth ($p<.06$). This difference between years can be explained by weather variation. The 1973 animals experienced a wider range of daily temperatures than in 1974, both lower minimums and higher maximums, and also fewer cloud-free days. Consequently, animals emerged later in 1973 (around 1000) compared to 1974 (around 0845). Since the site was shaded by 1400 hours, the daily periods of suitable basking was actually shorter in 1973 and the intensity of solar radiation diminished by cloud cover. The 1973 aggregation was also preceded by a very dry summer and fall. Food levels were quite low and perhaps insufficient fat was accumulated for maintaining high levels of basking activity.

Although no differences in daily frequency of basking were found, some evidence suggests that adult males bask for shorter periods than other age-sex classes. When the proportion of individuals seen in more than one census was calculated, the value for adult males was significantly lower (χ^2 for two independent samples, $p<.05$) than the other groups. Both adult sexes were less commonly seen in repeater censuses in 1973 compared to 1974, although the difference between years was significant for females only ($p<.01$). No differences were found among yearlings.

Because substantial proportions of an age class might be under-represented in the observations due to hibernation, a comparison of age structure between the aggregations and

the breeding populations on the "summer site" was made (Table 18). Yearling males were found in greater abundance than expected in the aggregations both years. This difference may result from the presence in the aggregations of males from marginal areas who had been excluded by the individuals holding territories in the optimal habitats (i.e., the summer site). Based on aggression data (Chapter II), one would expect a large proportion of these males from marginal areas to be yearlings. Adult males were less numerous than expected in 1973 and adult females less abundant than expeoted in 1974. This lack of consistency between years in the adult classes suggests no age class exclusively uses hibernation.

Short term hibernation is possible. The longest interval between sightings for some individuals was seven days. Other individuals were seen nearly every observation day. The wide variance in pattern makes generalization difficult.

Winter Growth

Lizards molt periodically when actively growing. The molt of skin removes the temporary paint marks used for identification of previously captured individuals. Thus, frequency of molting can be determined. Yearling S. jarrovi molt in early of mid-May shortly after the aggregations break up while all older animals molt in June or July. Growth records from study area yearlings measured in October and the following May indicated an average

snout-vent growth of 8.8mm for females (N=26) and 9.5mm for males (N=17). Because individuals that did not molt by the end of May were not included in this calculation, this estimate of winter growth may overestimate the actual gains of the entire population. Minimal yearling size in the fall is about 48-50mm but in the spring the smallest individuals are 53-54mm. Measurement of marked individuals indicates this shift in minimum size represents growth and not differential survival.

Immature females (under 54mm S-V) average more winter growth than mature female yearlings (Table 19) but the difference is not significant due to a wide variance ($0.1>p>.05$). Calculated in terms of proportionate increase per initial snout-vent length, immatures of either sex average greater growth than mature animals but the means are again not significant, due to the wide variance. However, rapidly growing immature animals would be expected to surpass slower growing mature animals. This explains the spring overlap in size between immature and mature females noted by Ballinger (1973).

The amount of growth can also vary between years. Yearling females grew about 2mm more in the winter of 1973-1974 than the winter of 1972-1973. Although the differences are not statistically significant ($0.1>p>.05$), it is interesting that this additional growth occurred during a winter when the female yearling age class was smaller in the fall ($p<.01$) than the previous year (1972). There is the

TABLE 18

THE AGE STRUCTURE OF BREEDING AND AGGREGATION POPULATIONS OF SCELOPORUS JARROVI.

	1973		1974	
	Breeding	Aggregations	Breeding	Aggregations
Adult Males	13 (21%)	12 (11%)	15 (26%)	34 (21%)
Adult Females	11 (18%)	13 (12%)	25 (43%)	45 (29%)
Juvenile Males	12 (19%)	39 (37%)	7 (12%)	39 (25%)
Juvenile Females	25 (41%)	43 (40%)	10 (17%)	38 (24%)
Total	61	106	57	156

TABLE 19

WINTER GROWTH IN YEARLING SCELOPORUS JARROVI

1973-1974.

	Females	Males
Immatures	8.83±10.26mm (17.77±.39%)	8.700±7.79mm (20.85±.55%)
	N = 18	N = 10
Matures	8.12±6.12mm (14.52±.19%)	10.714±14.90mm (15.50±.28%)
	N = 8	N = 7
Total	N = 26	N = 17

implication that immature females are utilizing fat reserves, which are destined for eggs in mature females, in achieving additional growth. Consequently, there are no differences in mean size of yearlings in the spring for each year.

Effect of Winter Basking on Parturition

Evidence that basking behavior expedites embryo development as suggested by Tinkle and Hadley (1973) comes from the correspondence between birthdate variance and the climatic conditions for each winter. One would expect early birthdates after warm, dry winters and late birthdates after cool, wet winters if winter basking enhances embryonic development among gravid females. Because weather varied dramatically during the study, a natural experiment occurred. Table 20 summarizes the parturition data and the weather observations, which generally agree with the above predictions. The deviation among years for the total degree-days during the gestation period is about seven (7%) percent. However, the order of magnitude in total degree-days does not correspond with the order of the parturition dates. Adjustments for rainy days and degrees over 32° C. did not alter this lack of correspondence. The number of degree-days for the basking period (November through April) do vary in the expected order for the three years. Since basking in May and June occurs in more shaded locations than winter basking, the degree-days for these months may have a less direct relationship to the pace of embryonic development. This would explain the disagreement in order between the total

TABLE 20

CLIMATIC PARAMETERS 1972-1974 AND PARTURITION DATES FOR TWO POPULATIONS OF SCELOPORUS JARROVI. DEGREE-DAYS ARE THE SUMMATION OF MAXIMUM TEMPERATURES RECORDED AT SAFFORD, ARIZONA (ELEVATION 885m) FOR THE PERIODS INDICATED.

	1971-72	1972-73	1973-74
Winter Type	warm, dry	cool, wet	warm, dry
Rainfall at Safford	3.45 cm	12.12 cm	2.99 cm
Gestation Dates			
1825m	May 21	June 21	June 2
2285m	June 25	July 7	---
Degree-Days (°C.)			
Nov. 1 - April 30	3809	3045	3690
Nov. 1 - Gestation Date	4443	4682	4769

gestation degree-days and the parturition dates. The disagreement may also result from using weather records from Safford, Arizona (885m elevation) rather than a more distant but elevationally appropriate location.

Animals at low elevations may benefit more by winter basking during warm winters than ones at high elevations. The more narrow yearly differences in birthdates for animals above 2285m may reflect less dependence on winter basking. Since higher elevations are associated with cooler temperatures, more snowfall, and greater cloud cover, animals at high elevation probably bask less frequently during the winter with resulting delays in embryonic development.

These observed altitudinal differences can be compared to the birthdates of eleven gravid females from various elevations which were kept in a warm lab during the winter. Parturition in this group occurred in March, with a gestation length of five months. The birthdates for the 1825m and 2130m females overlapped completely. The one 2300m female died on the last birthdate of the other animals. Upon dissection, its embryos were found to be completely developed with parturition to be expected in a few days. The closeness of the birthdates suggests the altitudinal differences in parturition are primarily the result of environmental conditions (the amount of winter basking possible) and not due to underlying genetic differences associated with developmental rates.

TABLE 21

CORRELATIONS BETWEEN CLIMATIC PARAMETERS AND PERCENT MATURATION OF YEARLING SCELOPORUS JARROVI AT 1825m.

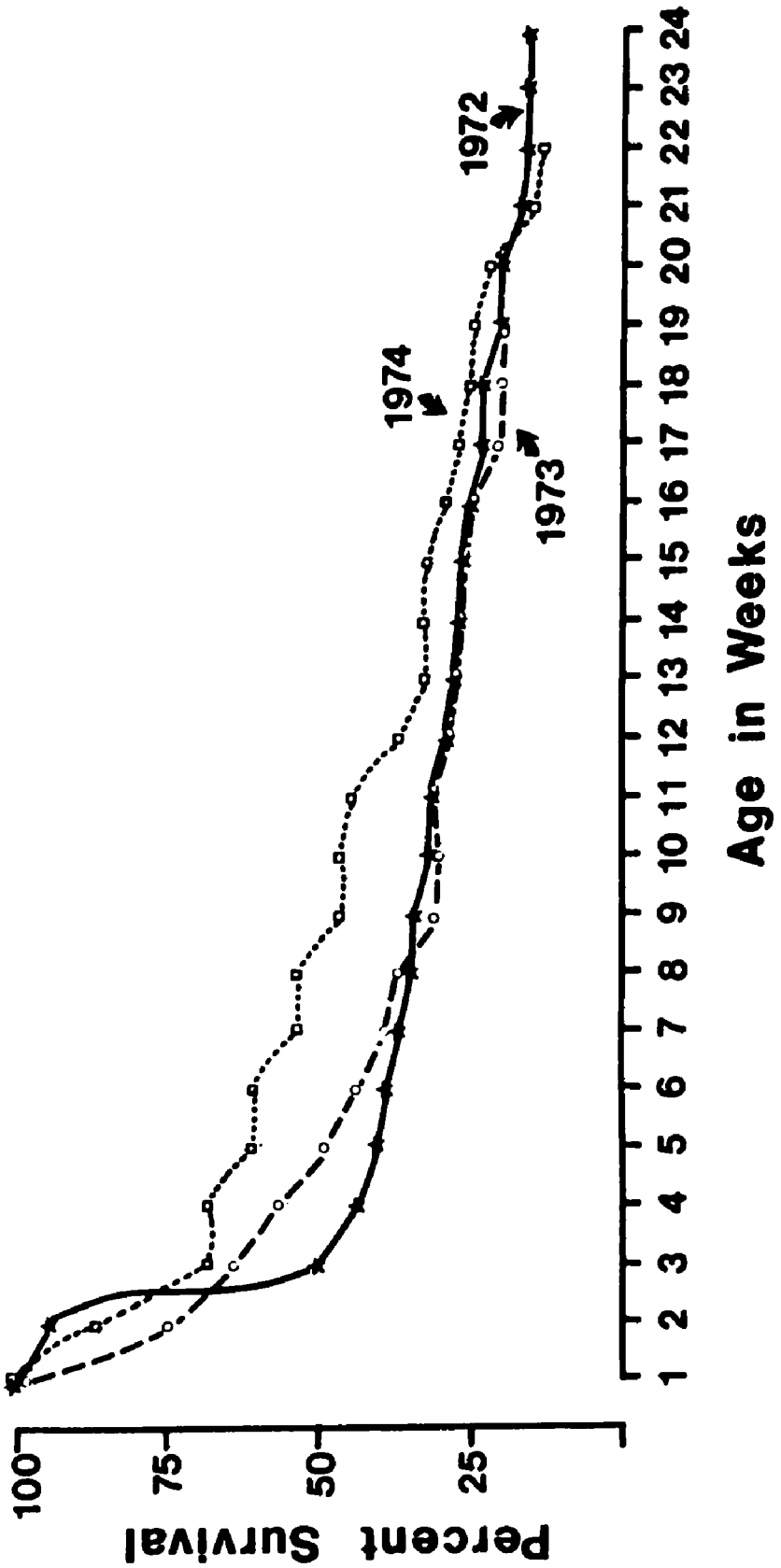
Year	Birthdate	Summer Rainfall	Female Mean Size	% Mature	Male Mean Size	% Mature
1972	early	heavy (25cm)	55.90	70%	56.41	76%
1973	late	light (7cm)	52.70	41%	55.73	70%
1974	average	moderate (17cm)	53.10	49%	56.84	80%

Early birthdates apparently enable greater numbers of young to reach sexual maturity in their first fall at the age of six months. Both sexes seem to reach sexual maturity around 54mm snout-vent length (See Chapter I). When the average October size of yearlings was calculated and compared with the birthdate and the amount of summer rain (Table 21), the late birthdates in 1973 corresponded with sharp reductions in the numbers of females that attained sexual maturity in their first fall. Since this year also received the least rainfall, the failure of some females to reach maturity may also reflect the lack of food resources. (See Chapter II for evidence supporting a correlation between rainfall and food abundance.) In contrast, the variance in birthdates did not appear to have effected survivorship of the young (Figure 27).

Given the reasonable assumption that gravid females are more susceptible to predation than postpartum females, earlier parturition dates should be favored. The increase in predator numbers with the emergence of various Crotalus species in late May should further increase the selective pressure upon the date of parturition. Greater mortality among females would be expected if parturition were late. However, survivorship figures from May 1 to the 50% parturition date for each year do not fully agree with this expectation. Survival was highest in 1972 with the shortest gestation but survival during 1974 was not intermediate in value as would be expected from the intermediate duration

Figure 27: Patterns of survivorship among first year animals 1972-74. Survival was calculated weekly. Week one represents the date when about 50% of the females in the study area gave birth.

Figure 27


1972
1974
1973
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Age in Weeks
100
75
50
25
Percent Survival

of gestation. A more precise measure of survival would be determining the mortality, within one year, of females with early parturition compared to those with late parturition. Dates of parturition could not be established with accuracy for many study area females. Individuals were frequently absent for several days prior to being noticed as postpartum. Also, yearling females showed little obvious external change when newly postpartum, unlike older females who looked wrinkled and collapsed.

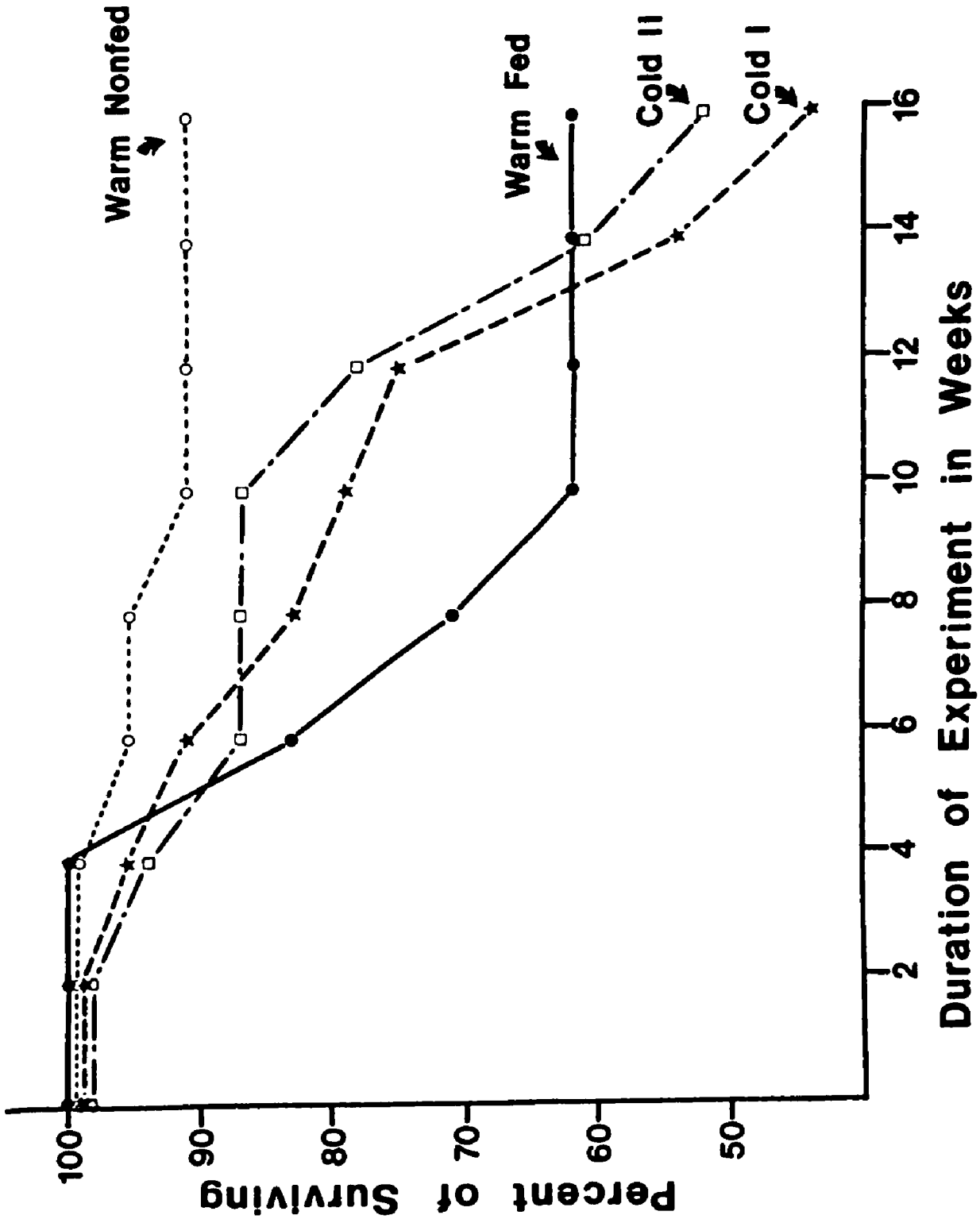
As a result of later birthdates and less (slower?) growth due to a shorter warm season, the high elevation animals do not mature in their first fall. At these elevations, minimum size for sexual maturity is around 70mm at an age of fifteen months (second fall). Collecting at various elevations in the fall of 1972 and 1974 revealed that no first year animals were mature above 2100m elevation.

Laboratory Hibernation

In the laboratory test, animals in constant cold suffered greater mortality than animals in fluctuating warm and cold conditions. The survivorship curves for each group are shown in Figure 28. The warm unfed group (control) had a survivorship approximating field conditions. Both cold groups suffered the greatest mortality and the experiment ended when mortality reached 50% in one cold group. Surviving animals could not be distinguished from those not surviving on the basis of initial body size, body weight or elevation of origin. The declining survivorship in the warm

Figure 28: Survivorship in four groups of gravid females subjected to different regimes of temperature and food. Each group had the same inital sample size.

Figure 28


Warm Nonfed
Warm Fed
Cold II
Cold I
Percent of Surviving
100
90
80
70
60
50
Duration of Experiment in Weeks
2
4
6
8
10
12
14
16

fed group until halfway through the experiment is unexplainable. Both warm groups appeared to have become adjusted to the lab conditions by February 1, as mortality ceased and animals in these groups began regaining weight previously lost (Figure 29). Since the warm unfed group had access only to water, this weight gain must represent water replacement. Animals which died during the experiment averaged a weight loss of 37.5% (range 9-46%) from their starting weight. This far exceeds the 15-20% weight loss of surviving animals in the cold groups.

Data from dissected animals (Table 22) indicate several insignificant differences between the groups. However, fat body weights did differ significantly between the two warm groups, with the warm nonfed group having smaller fat bodies as a result of food deprivation during the experiment. Fat body weights did not correspond to mortality losses, as the group with the lowest fat body sizes had the lowest mortality. This suggests that mortality results from more than depletion of fat body reserves. The significant difference in average egg weight reflects the embryonic development which occurred in animals from the two warm groups.

Figure 29: Patterns of weight loss among animals who survived the laboratory experiment. Values shown are means $\pm$ 1 S.E.

Figure 29

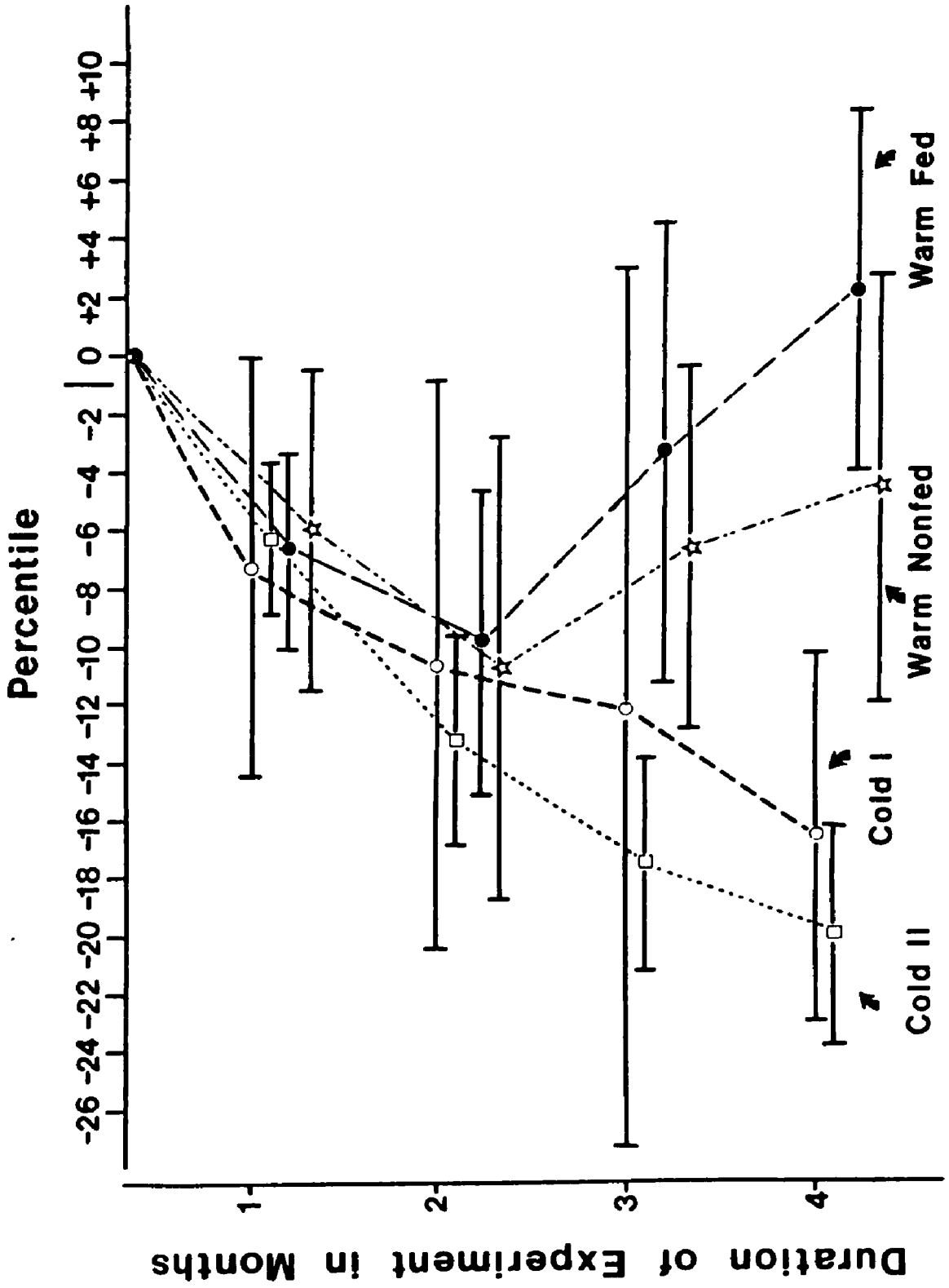

Percentile
+10
+8
+6
+4
+2
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
1
2
3
4
Duration of Experiment in Months
Warm Fed
Warm Nonfed
Cold I
Cold II

TABLE 22

DIFFERENCES BETWEEN EXPERIMENTAL GROUPS OF *SCELOPORUS JARROVI* MAINTAINED UNDER DIFFERENT REGIMES OF TEMPERATURE AND FOOD.

Measure	Cold Group (1)	Warm Nonfed Group (2)	Warm Fed Group (3)	Test
Starting No.	47	23	24	
Sample Size	12	6	6	
Starting Body Weight	14.57±3.52 g	13.88±4.27 g	14.34±3.07 g	NS
Final Body Wt.	12.17±2.99 g	11.89±3.17 g	14.513±2.07 g	NS
Total Clutch Weight	2.070±.575 g	2.123±.820 g	2.426±.536 g	NS
Litter Size	7.41±2.15	6.50±2.16	6.83±.75	NS
Fat Body Weight	0.0412±.0263 g	0.0211±.01624 g	0.0823±.0525 g	2<3 p<.02
Egg Wt/BW	.1696±.0210	.1748±.0280	.1664±.0226	NS
Average Egg Wt.	0.2810±.0264	0.3246±.0517	0.3523±.0518	1<2+3 p<.002
Percent Fat Body/BW	.0033±.0019	.0016±.0008	.0054±.0031	2<3 p<.01

DISCUSSION

All age groups and both sexes of Sceloporus jarrovi bask during the early winter, with roughly equal frequency, while aggregated on sunny rock cliffs with deep crevices. Adult males seem to bask for shorter periods of time. A multiplicity of functions accompany winter activity.

By raising body temperatures to high levels, basking during the winter by gravid females enhances the embryonic developmental rate, which is temperature dependent in reptiles (Defaure and Hubert, 1961). The correlation between gestation length and degree-days for the months while aggregated (November through April) suggests a simple, direct effect of the heat absorbed during winter activity upon the development of embryos. Consequently, the variation in parturition demonstrated here and the reported differences in development during the winter months (Goldberg, 1971; Tinkle and Hadley, 1973) can be explained as the results of climatic variations in different years. Furthermore, the elevational differences in gestation length appear to result from environmental factors rather than genetic limitations. When incubated under identical conditions, the young of females from different elevations are born at overlapping times and the field differences in birthdate disappear.

Selective pressures for shortening gestation times and encouraging female basking are the avoidance of predators and increased reproductive potential. The high winter

survivorship suggests that risk during this period is quite low. Predation probably becomes significant in May and predator densities further increase in late May with the emergence of various rattlesnake species (Crotalus). By shortening gestation, basking behavior reduces the length of exposure of near-term females to predators. This assumes, reasonably, that non-gravid or postpartum females would escape predators more successfully. The inability to correlate differences in spring survivorship between years with gestation length may result from the relatively small samples, from not being able to confidently separate mature and immature females in the spring, and from between-year differences in predation pressures. The ideal measure would compare females' dates of parturition with their survivorship within one year but logistic difficulties prevented obtaining this data. Further complicating an assessment of the impact of predation upon gestation length is the possibility that climatic factors which affect developmental rates of embryos in the spring may also delay emergence of reptilian predators or alter searching patterns of avian predators, thus cancelling out the predation pressure on parturition dates among present populations. However, survivorship data from other months (unpublished data) indicate that a more prolonged gestation would result in significantly higher mortality.

An individual with an early birthdate has a higher probability of reaching sexual maturity in its first fall.

By shortening the generation time in this way, the basking behavior increases the reproductive potential of the parents (Lewontin, 1965). This effect should be the primary selective pressure favoring winter activity in females.

Basking behavior also prolongs the growing season for animals at 1800m (study area elevation) and substantial additional growth is attained by first year animals in the winter. The observed increase of 15-20% in body length by yearlings would be vital in a breeding system where larger body size confers a large competitive advantage for reproduction among males (see Chapter III) and increases litter size in females. Litter size increases roughly by one for every increase of three mm in body length of adult (two-year old) females (Ballinger, 1973). Although much smaller growth increments occur in larger males (two years and older) than in yearling males, the advantages of any growth seem to outweigh the risks of basking. This difference in growth potential between age-classes may explain the high proportion of repeaters among yearling males compared to older males, since the potential gain is greatest in yearlings. Consequently, the reproductive gain from winter growth has favored winter basking behavior rather than prolonged hibernation.

This winter growth is in sharp contrast to other lizard species which generally have minimal or no growth during cold periods. However, Crenshaw (1955) reported small yearling Sceloporus undulatus grew more during the winter

than larger juveniles, which he attributed to the smaller animals' delaying hibernation in the fall, emerging more frequently during the winter and becoming active earlier in the spring. Davis (1967) found an inverse correlation between size and winter growth in female S. occidentalis.

Summer survivorship of young does not appear to vary according to the birthdate but the birthdate does effect their reproductive potential. Late birthdates prevent some young from maturing in six months. This can be partially offset by growth in October and mating in the aggregations as occurred in 1973. However, at higher elevations (above 2100m), the shorter growing season and/or slower growth rates prevent maturation in the first year. Compensatory increases in survivorship or fecundity should be expected in high elevation populations.

The failure of some individuals to mature in their first fall will reduce their reproductive potential in that year compared to early maturers. If the observed dimorphism in age of maturity at 1800m has a genetic basis, it may be maintained by genetic "swamping" from the high elevation populations, or by fluctuating conditions that favor delayed maturity in some years. However, the variation in age of maturity may be phenotypic and reflect differential growth rates produced by demographic and competitive factors. Since the observed variation in initial body size (26-28mm) and birthdates (range of 10 days) is rather small, these factors are probably not important in producing the

variance in juvenile body size observed in October (48-66mm SVL at 1800m). Rather, differential growth rates resulting from the range in food quality between territories would contribute to the variance in body size.

Plasticity in age of maturation may be adaptive in certain life history strategies (Wilbur and Collins, 1974). In S. jarrovi, the decision to divert energy from further growth into reproduction in the first fall probably involves several factors: 1) the current rate of growth, 2) the energetic requirements of reproductive effort, and 3) the requirements for accumulating adequate food reserves for the winter. The current rate of growth will determine whether the animal can reach minimum size before breeding activity ends. The earlier in the year the minimum size is reached, the more likely successful reproduction can occur. Since there is little variance in clutch size among yearlings (Ballinger, 1973), the reproductive requirement would be proportionately greater for females just reaching the minimum size than larger yearling females. The energetic demands of reproduction (particularly gametes formation) may be much less for yearling males, allowing greater conversion of energy into growth, as suggested by their larger mean size in the fall (Table 21). The energetic requirement for winter basking may be most crucial, as insufficient levels of food reserves would not assure survival through the winter, making the reproductive effort futile. Circumventing this food requirement by hibernating would have disadvantages, as I have shown above.

The interacting and generally conflicting demands on the energy budget suggested by this analysis should favor plasticity in the age of maturity. The animal must weigh the gain of reproducing in the first year against various costs or requirements for reproduction and survival through the gestation period. Accumulating sufficient energy to achieve the minimum body size with adequate resources for reproduction and winter survival may place the animal in an intense competitive position against conspecifics or increase the exposure to predation. Because of the widely varying growth rates in yearlings, the decision to reproduce will be advantageous for some individuals, who have attained adequate size. For others, their fitness might be maximized by conserving all resources for growth and winter survival thereby postponing reproduction until the next year. Because of the greater energetic investment in gamete formation by females, one might expect to find greater plasticity in age of maturity in that sex, expressed as greater variance between years in the proportion of females reaching maturity at six months.

Hibernation for the entire winter is apparently not desirable for S. jarrovi, although some short-term dormancy may take place. While some individuals can withstand cold conditions, more animals died under this stress as demonstrated in the laboratory experiment and the animals forced to hibernate emerged in poorer physical shape compared to non-hibernating animals. After the termination of the lab

experiment, the cold group animals continued to suffer greater mortality during the first two weeks of warm conditions than the two warm groups. This suggests that, without physiological changes, S. jarrovi which hibernated would emerge in poorer condition than basking individuals. The apparent adequacy of fat reserves in S. jarrovi contrasts with Weintraub's (1968) suggestion that S. orcutti juveniles have insufficient resources and must feed during the winter. However, yearling S. jarrovi do generally incur greater mortality during the winter than older adults. These yearlings may have insufficient reserves for winter activity or attempt to hibernate.

Death in cold conditions does not occur from depletion of the fat body reserves alone. The extent of fat body losses did not correlate with mortality in the lab experiment. The cold group suffered the greatest mortality but presumably used the least fat reserves. By contrast, the warm unfed group which lost the most fat body weight suffered the least mortality. In addition, the weight loss of dead animals far exceeded the weight of the fat body. Mortality during cold conditions may result from dehydration, accumulation of metabolic wastes, or a more complete depletion of all body fat. Elimination processes were shut down in the cold group animals and they were not mobile enough to use available water.

Basking behavior may have selected for some small morphological changes. The advantage of heat absorption

during the winter months may explain the reduced scale overlap noted in S. jarrovi by Regal (1974). The heat shield function proposed for such scale overlap in other lizards would defeat the purpose of basking proposed here for females. One can speculate that winter basking would be important for other small-scaled members of the Sceloporus torquatus group (Smith, 1936) with similar life cycles to S. jarrovi, but not important for the large-scaled members.

The fall ovulation in S. jarrovi (Goldberg, 1971) and other closely related species (Crisp, 1964; Ballinger, 1973) is unique among known lizard life histories. The selective forces that favored this distinct reproductive cycle, rather than a less modified system, such as reported for Gerrhonotus (Vitt, 1973) which also shows winter activity, cannot be identified at present. Certainly year-round activity would make the evolution of fall ovulation possible.

In a survey of lizard life histories, Tinkle, Wilbur and Tilley (1970) identified two general reproductive strategies: 1) early maturity, multiple clutches and 2) late maturity, single clutch. Several exceptions, including S. jarrovi, have recently been found to this proposed dichotomy (Ballinger, 1973; Tinkle 1973). It appears that behavioral adaptations contribute to the unique strategy used by S. jarrovi. Therefore, to the growing list of factors that may effect the evolution of life history strategies (Wilber, Tinkle and Collins, 1974), one must not overlook behavioral solutions to adaptive strategies.

APPENDIX I

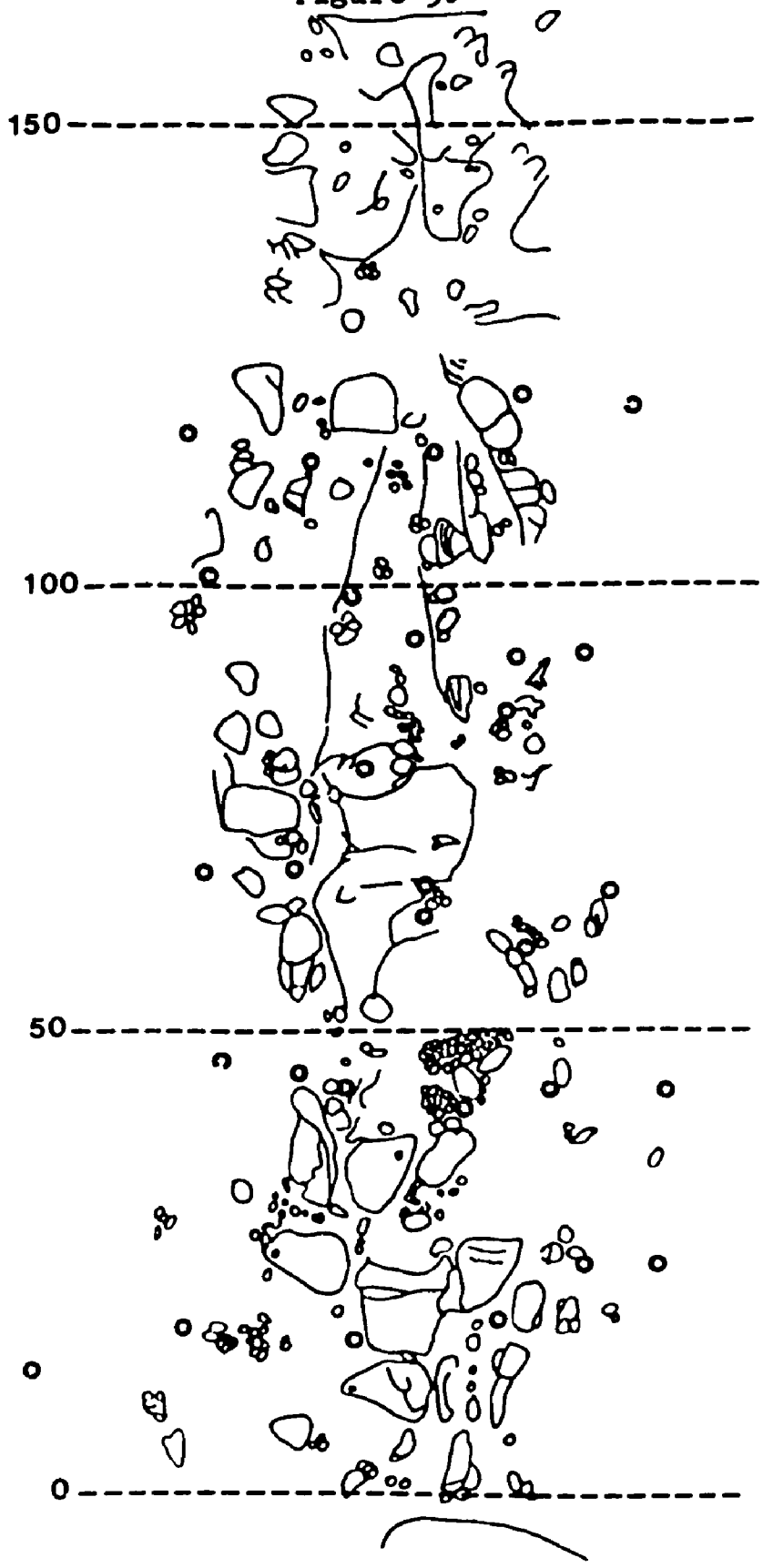
MEAN TEMPERATURES (°C.) AND TOTAL RAINFALL (mm)
AT SAFFORD, ARIZONA (ELEVATION 575m) 1972-74.

	1972			1973			1974		
	Mean Max.T	Mean Min.T	Rainfall	Mean Max.T	Mean Min.T	Rainfall	Mean Max.T	Mean Min.T	Rainfall
January	16.4	-3.6	0.0	13.5	-2.0	0.6	15.6	-1.0	10.9
February	20.9	-1.9	0.0	15.7	1.7	54.9	18.0	-3.8	1.5
March	27.3	5.0	1.0	17.0	2.8	37.3	23.4	3.4	2.5
April	28.4	4.9	0.0	23.1	4.1	0.7	26.7	5.5	1.5
May	31.8	9.6	6.1	31.0	10.8	19.8	32.8	10.7	3.6
June	36.0	16.5	6.8	36.0	15.8	14.0	39.5	20.7	42.4
July	37.8	20.7	42.4	36.9	19.9	37.3	35.6	19.8	73.4
August	34.8	19.3	65.8	36.9	18.8	24.4	35.0	17.8	19.8
September	32.6	15.5	46.5	34.1	12.7	2.0	31.4	15.7	49.8
October	25.1	11.5	93.5	29.5	7.3	0.0	25.5	10.9	37.3
November	17.5	0.7	12.5	21.8	0.6	5.6	20.2	2.0	4.5
December	4.3	-2.1	10.1	17.1	-4.0	0.0	16.6	-3.6	0.0

APPENDIX II

Figure 30. A map of the "summer site". Locations of large rocks and the thirty locations where stiky insect traps were placed are shown. Numbers indicate the linear distance, in meters.

Figure 30



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