

AN EXPERIMENTAL STUDY OF COLLARED LIZARDS:
EFFECTS OF HABITAT AND MALE QUALITY
ON FITNESS

By

MARGARET ANNE ROSTKER

Bachelor of Science
Oregon State University
Corvallis, Oregon
1977

Master of Science
Oregon State University
Corvallis, Oregon
1980

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Thesis Approved:

[Signature]

Thesis Adviser

[Signature]

Anthony A. Eckel

[Signature]

Larry B. Tabb

[Signature]

Norman A. Durbin
Dean of the Graduate College

PREFACE

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INTRODUCTION

Theories on sexual selection are only slightly less disputed than those on natural selection. The two are often inseparable and there appears to be little consensus as to whether sexual selection is subsumed under natural selection or is a legitimately separate type of selection. Darwin himself recognized the continuity of these two selective forces when he first set forth the fundamentals of natural, and later, sexual selection (1859,1871). While arguing that sexual selection could explain certain sexual characteristics patently detrimental to individual survival, he admitted the difficulty in distinguishing which among such characteristics were products of sexual and not natural selection. Nevertheless Darwin attempted to distinguish between the two selective forces. Wallace (1889) and Huxley (1938) disagreed that sexual selection was of any consequence, and both maintained natural selection alone satisfactorily explained observed sexual dimorphisms and mating strategies. Both adamantly argued against the notion that female choice could positively promote male characteristics.

Fisher (1930) however, theorized that both inter- and intrasexual selection (sensu Darwin 1871) were agents in shaping phenotypic and reproductive characteristics. Darwin described two forms of sexual selection as 1) a struggle between males for females and 2) female choice of mates. The two patterns are now widely viewed as 1) intrasexual selection, or competition within one sex for individuals of the opposite sex and 2) intersexual selection, or preferential choice of mates by one sex relative to the other (Thornhill 1979). Run-away

selection was hypothesized responsible for those secondary sexual characters that appeared extremely ill-adapted for individual survival, yet were obviously important in the promotion of superior reproductive success.

Reflecting upon inter- and intrasexual variations in morphology and behavior, Darwin noted the apparent "eagerness" of males to mate and "coyness" of females in resisting male attempts (1871). He hypothesized that disparate fitnesses would accrue between and among the sexes, with most females mating and producing a species characteristic number of offspring. Males, however, would show serious discrepancies in reproductive success, and this would nowhere be more pronounced than in polygamous species where a single or few males could gain control of breeding opportunities and exclude most other males from direct genetic contribution to future generations.

Bateman (1948) provided laboratory evidence in support of unequal variances in fitness between the sexes. His classic breeding trials with Drosophila clearly demonstrated that the sex with least investment in reproduction (males donating 'cheap' sperm versus females producing 'expensive' eggs) will show the larger variance in reproductive fitness. Most, if not all, females will find males to fertilize their eggs whereas not all males will find receptive females. Williams (1966) elaborated upon the investment differences between the sexes and theorized how selection would promote male salesmanship (of sperm) and female discrimination for mates. Thus courtship strategies would differ between the sexes in accordance with differential primary germ cell energetics.

Parental care components were incorporated into sexual selection

theory by Trivers (1972) who observed that intrasexual male competition for mates would select against male parental investment beyond gametic contributions. Females, on the other hand, would be selected to favor greater male expenditures in terms of material benefits (e.g. food, defense, help in raising young) above and beyond initial sperm donation. Trivers theorized separate investment curves for the sexes and showed a strategic continuum from monogamy to polygamy in terms of differential energetic investment and parenting responsibilities between the sexes.

Recent work on sexual selection has often focused upon cost-benefit criteria for mate choice by females. Researchers have stressed female mate choice predicated upon perceived benefits to offspring as especially useful in work with non-monogamous species. Mate choice categories are based upon genotypic and material benefits. Female choice criteria based upon genetic benefits is well-documented by Fisher 1930, Williams 1966, Orians 1969, Trivers 1972, Borgia 1979, Weatherhead and Robertson 1979, Yasukawa 1981 and Loiselle 1982, among others. Mate choice as determined by material benefits is described in Verner 1964, Verner and Willson 1966, Zimmerman 1966, Lack 1968, Orians 1969, Wittenberger 1976 and Hogstedt 1980, and elsewhere.

Borgia (1979) notes that in cases where genetic benefits are the choice criteria, the choosers (usually female) may rely on intrasexual competition among males to identify superior mates and not so concern themselves with comparison shopping. However, in cases where material benefits are offered to females by prospective mates, females will gain by careful mate selection predicated upon both sets of criteria. Females may be forced to compromise between males with high genetic quality (demonstrated phenotypically) but poor material resources (a

poor quality territory, for example). Borgia (1979) suggests that female mating decisions in such cases will be based upon the relative value the female assigns to each type of benefit, and also the degree of correlation between the two kinds of benefits a male may offer.

Given that males in general experience the greater variances in fitness, Williams (1975) predicts the highest variance in male reproductive success will occur in those mating systems wherein females base mate choices solely on genetic benefits. This is so because females, likely to use similar criteria in choosing, will favor only a subset of all available males, namely those individuals who have somehow demonstrated genetic superiority relative to the others. Additionally, a male who provides only sperm should rarely be limited in his ability to fulfill female demands, and thus usually mate with as many females as choose him (Orians 1969). On the other hand, material benefits (e.g. food, nest sites, defense ability) may be gradually depleted as a male offers them to mates and thus the residual value of benefits a male can offer other females is reduced. In material benefit systems it is more likely that variances among male fitnesses will be relatively small (most males can obtain, hoard or control about the same amount of resources, hence mates) except under certain conditions of resource clumping where one or a few males manage to hold all or most materials important to females (Borgia 1979).

It is likely the two kinds of benefits are correlated (Wittenberger 1976, Heisler 1981, Weatherhead and Robertson 1981, Waltz 1982). Widely recognized models of mate choice admittedly confound the criteria and frequently conclude with calls for experimental work that separates the two to determine their

importance in mate choice and reproductive success (see polygyny threshold models by Verner and Willson 1966 and Orrians 1969, war propaganda model by Borgia 1979, and sexy son model by Weatherhead and Robertson 1979). Theory abounds supporting one or the other criterion but quantitative data supporting one type of benefit while controlling for the other remains rare or altogether lacking.

This paper reports a field experiment designed to separate material benefits (territory quality) from genetic benefits (intrinsic male quality) as a basis for mate choice in lizards. Using an experimentally homogeneous enclosure (treatment) and heterogeneous natural sites (controls) I compare mate selection and resultant fitnesses under two sets of conditions. The enclosure offers only individual variations in genetic benefits (morphology and behavior) as a basis for choice. The natural colonies contain variable habitat (hence, territories) in addition to individual variations in genetic quality and thus mate choice may be based upon either or both criteria. I derive a size-specific fecundity model to predict female fitness and use spatial and temporal overlap of males with females to estimate male fitness. Using these estimates of fitness, I compare the degree to which heterogeneous habitat features (material benefits) explain the observed pattern of male fitness above and beyond the morphological characteristics (genetic benefits) of the males. Additionally, the influences of behavior, morphology and consort characteristics on fitness are examined with respect to the experimental design.

The organisms used in this study are collared lizards (Crotaphytus collaris). Like many lizard species, they are well-suited for ecological and theoretical research (Tinkle 1967). Importantly, neither

sex provides any known form of parental care beyond egg deposition (but see Fitch 1956, for speculation on female defense of nest areas). This feature of collared lizard life history means female choice is most likely limited to the two criteria of intrinsic male quality (evidenced in male morphology and behavior) and material benefits (defense against other lizards and quality of resources on defended areas, including perches, prey and refugia). Sedentary, social and territorial (Fitch 1956, Mosley 1963, Yedlin and Ferguson 1973), these lizards occur in high densities in localized areas and thereby further facilitate experimental work requiring manipulation and observation of free-living individuals.

LIFE HISTORY

Collared lizards (Iguanidae: Crotaphytus collaris) are social, aggressive insectivores with stereotypic behaviors (Mosley 1963) and intense territoriality (Yedlin and Ferguson 1973). Although they are relatively large (adult male body lengths up to 115 mm), brightly colored organisms, and range from the southwestern United States into Mexico (Conant 1975), collared lizards are poorly known. Studies have tended to emphasize taxonomy (Burt 1928, Fitch and Tanner 1951, Axtell 1972, Smith and Tanner 1974), diet (Pack 1923, Blair and Blair 1941, Banta 1960) and physiology (Weiner and Smith 1965, Cole 1966, Wever and Werner 1970, Cooper and Ferguson 1972). Documentation of their longevity, fecundity, productivity, habitat and social systems remains incomplete.

Collared lizards are sexually dimorphic with the males up to one-third larger than females and more brightly colored. Body

proportions are different between the sexes: males have relatively larger and broader heads, more massive jaw muscles, wider tail bases and proportionately longer tails (approximately 130% of body length) than the smaller, slimmer females (Bontrager 1980). Both sexes exhibit stereotypic motor patterns of throat fans, lateral flattening, back arches, gaping and bipedal locomotion, though certain behaviors, notably those of aggression and courtship, are more intensely and frequently performed by males (Mosley 1963, Yedlin and Ferguson 1973). Both sexes are thought to be territorial, males the more so with larger and more thoroughly defended territories than females.

These lizards occur in colonies of two to 20 or more and are invariably associated with rocks or boulders. Generally considered polygamous, there are few details on harem size, female role in determining harem size or the relative benefits accrued by the two sexes in such a mating system.

Sit and wait predators, collared lizards feed primarily upon orthopterans and, secondarily, coleopterans. Smaller lizards, including hatchling collared lizards, may be taken as well.

Reproductive information is scarce and consists primarily of generalizations in the literature. Minimum size at maturity is about 92 mm snout-vent length; lizards may breed following their first hibernation (Tinkle, Wilbur and Tilley 1970). The average clutch size is six eggs, with larger, older females producing larger clutches (Vitt 1977). Mean egg size is 20 mm by 13 mm (Clark 1946). Eggs are laid 16-19 days after copulation (Vitt 1977). A second clutch may be laid two to three weeks after the first, though it is not known how often this occurs. Collared lizards have seminal receptacles in oviducts

(Montanucci 1974) and it is not known if remating is necessary between first and second clutches, or even every reproductive season. Eggs are buried in loose soil, and temperature dependent incubation ranges from 51 to 94 days (Parker and Pianka 1976). Robinson and Tanner (1962) note that ovarian counts are not correlated with number of eggs laid, as tiny eggs are still present when others are ready to be laid. First clutches are usually laid in mid to late July, second clutches well into August.

Females and smaller individuals emerge first from hibernation in April with males following in about two weeks (Fitch 1956). By late May or early June courtship is intense. Male spermiation occurs then, and cycles again in late July and August (Parker 1973, Trauth 1979). Gravid females are first seen in late June, with oviposition occurring several weeks later (Fitch 1956). By early August adults have begun hibernation, juveniles and hatchlings follow in late August, September and October (Fitch 1956, Bontrager 1980).

METHODS

Study sites

The Wichita Mountains of southwestern Oklahoma are noted for their dense populations of collared lizards. My study sites were on the west range of the Fort Sill Military Reservation, Comanche County, in the Wichita Mountains Biotic District (Blair 1939) of the Rolling Red Plains (Gray and Galloway 1959).

Grasslands dominate the habitat. Tall grass species include Big Bluestem, Little Bluestem and Indian Grass (Andropogon gerardi, Schizachyrium scoparium and Sorghastrum nutans, respectively). Mid and short grasses include Blue Grama and Buffalo Grass (Bouteloua gracilio

and Buchloe dactyloides). Wide-spread forbs are Western Ragweed (Ambrosia psilostachya), Blanketflower (Gallardia pulchella), and Sneezeweed (Helenium amarum) (Crockett 1962). Post Oak (Quercus stellata) and Blackjack Oak (Q. marilandica) are common along streams while Eastern Red Cedar (Juniperus virginiana) is abundant and wide-spread.

The climate is temperate-continental of the dry, subhumid type (S.C.S. 1967). Due to high winds and temperatures there is a high evapotranspiration rate. Seasonal changes tend to be gradual and variable from year to year (Waldrip 1977). Annual precipitation averages 73.4 cm, with 34% of the total falling in spring, 27% in summer, 24% in fall and 15% in winter (S.C.S. 1967). Yearly snowfall ranges from 12.7 cm to 18.8 cm on the long-term (30 year) average. Long-term average temperatures in January are 3.2°C and 27.2°C in August (N.O.A.A. 1958-1977).

I studied three natural colonies of collared lizards and one colony in an experimental enclosure, all on the west range of Fort Sill and within 10 km of each other. Two of the natural sites were road-side cuts along little-used roads. In both cases large rocks were abundant in bare ground patches and native vegetation surrounded the approximately .5 ha sites on three sides. The largest of the natural sites at .8 ha was located on a flat, grassy hilltop between two gently sloping drainages. It contained scattered rock outcrops amidst grasses and forbs. All natural sites were inhabited by free-living lizard populations which were unmanipulated through the study. Natural boundaries of unfavorable habitat were used to define the sites, and resident lizards were quite site tenacious. I detected very few

transient lizards on these sites; the few found were juveniles, and probably immigrants.

I located the 1 ha experimental site on a flat (slope $< 5^\circ$), grassy expanse near the natural sites. It was fenced with metal sheets (75 cm X 3.5 m) nailed to flat stakes along the outside. A 20 cm asphalt strip lined the interior fence base to prevent burrowing escapes.

The enclosure was graded to bare ground, leaving a continuous 3 m strip of vegetation along the fence and two large triangular patches of natural cover (Figure 1). The slight lack of symmetry was due to the originally undetected presence of partially buried boulders that the grader could not move without creating large holes. Each season I thoroughly cleared the enclosure of snakes.

In 1981 I arranged 15 identical rock piles of seven cinder blocks in a regular pattern (Figure 1). Each cinder block measured 20 cm X 20 cm X 40 cm and had two holes. In 1982 I used 30 rock piles of five blocks each and five of three blocks. Lizards readily accepted the piles and I observed no preference among the three-, five- or seven-block piles. Within each pile size, I arranged each pile of cinder blocks to offer identical north, south, east and west basking slopes, similar maximum perch height and a consistent number of holes and cover entrances. I provided as homogeneous an environment as possible in the enclosure with respect to perch size and distribution, cover, vegetation, food and predation pressure.

In 1982, for reproductive information, I collected 82 female collared lizards from Fort Sill and the adjacent Wichita Mountains National Wildlife Refuge. All females were collected within 30 km of the study sites, none closer than five km to any one site.

Habitat

Collared lizards rarely venture more than a few meters from their perches except when relocating to a different perch. These perches are almost always in patches of bare ground, and while they are mainly rocks, any kind of topographic protrusion may be used. Most foraging is in the immediate vicinity of the perch, although some lizards will move into tall grass four or more meters away. While some individuals will enter very grassy areas I never found them far from a site offering cover and a perch. Mostly I found collared lizards living in areas of scattered grasses with rock perches. It is almost always on or near such a perch that aggression, defense, courtship and copulation occurs (Mosley 1963, Yedlin and Ferguson 1973).

Since perches appeared so important, I systematically sampled the habitat around perch sites. Four sampling transects ran from perch center 3 m out in the cardinal compass directions. I recorded linear amounts of bare ground, grasses and forbs. I noted perch height and diameter and mapped the areas.

Semimonthly walking counts of grasshoppers were made in the bare and grassy patches to assess prey abundance. On each site and in the enclosure I walked continuously for one minute in each patch type and counted all the orthopterans I observed or flushed. These prey counts were limited to still, sunny days and I sampled all sites under similar conditions and within one day of each other.

Morphology

Twelve variables of body size and condition were taken on all subjects. These include snout-vent length (SVL), tail length (Tail L), horizontal mouth gape (Gape), tail base width (Tail W), head width (Head

W) and weight (Mass). Mass was noted to the nearest gram, all other measurements were taken to the nearest mm. I also recorded four subjective indices of condition: thigh fat (Thigh F), tail fat (Tail F), femoral pore protrusion (Femoral) and body color (Color). The subjective indices were coded on an arbitrary scale of 0-4. I palpated all lizards for number of food boli and, for females, eggs.

I used toe-clip combinations to permanently identify individuals and dorsal paint codes for field recognition (Tinkle 1967). The paint codes were lost at each molt, and as lizards were recaptured for remarking they were generally weighed and palpated. In the final days of each season a special effort was made to catch and remeasure all subjects.

In the 1982 season I collected reproductive information on 82 females captured off the study sites. This group was caught by hand or noose and sacrificed by sodium pentathal injection, approximately 10 per week. I measured egg and bolus lengths and widths, and noted egg stage and fat bodies.

Behavior

This study incorporates approximately 250 hours of field observation of collared lizards. Vision is keen in these animals (Sugarman and Hacker 1980) and, to avoid observer bias, methods necessarily included a good deal of stealth. In general I tried to unobtrusively work my way close enough to observe subjects and their activity in 10-minute increments. With the natural colonies I could, in some cases, closely approach by vehicle and not disturb them. In other cases I approached on foot. For cover I constructed blinds beyond the four walls of the enclosure and used boulders and tall grasses on

the natural sites.

I always recorded time and location of a sighting and any neighboring individuals (≤ 20 m away). Periodically, if I considered my presence was not influencing action, I also recorded individual behavior. I noted 11 behaviors (Figure 2), which I based on personal observation (see below) and the literature (e.g. Mosley 1963, Carpenter 1967, Yedlin and Ferguson 1973). These include stereotypic iguanid motor patterns, body maintenance activities (e.g. basking, foraging) and social displays (aggression and courtship). I quantified each behavior as a percentage of occurrence to the total number of behavioral events recorded on a subject. I combined associated behaviors into 4 behavioral suites: aggression, maintenance, courtship, and general activity (Figure 2). The aggression suite is a summation of the display, chase, fight and patrol observations; maintenance is the sum of bask, alert bask and forage; courtship the sum of touch, mount and patrol; and activity is the sum of alert bask, alert, active (movements ≥ 1 cm) and patrol. I could not assign reasonable motive or intent to the behaviors of alert bask or patrol and so included them in more than one suite.

Field observations were made from May to early August in both years. Treatment observations were made in July of 1981 and from early June to mid-August in 1982 with almost daily observations of the lizards. On alternate visits I either noted time and location only (a census) or made behavioral observations in 10-minute increments. If I was observing behavior, I went directly to a randomly selected blind. Upon my appearance at the blind, nearby lizards usually withdrew into the nearest rock piles. After 10 to 20 minutes they would reappear and

after another 10 minutes usually resume regular activities. I waited for their resumption of routine behavior before beginning my observations.

On census days I stepped, prominently in view, into the enclosure and drove all lizards into the closest rocks. Having thus frozen them in space relative to one another I then systematically searched each rock pile and noted individual locations.

In 1981 I spent about 100 hours observing control colonies and another 90 watching treatment lizards. In 1982 I observed treatment lizards for 20 hours to determine if their behavior was any different from the previous year. I observed control colony behavior for 40 hours in 1982 to determine social relationships.

Fitness

Fitness for females was estimated from a size-specific fecundity model (Ruby 1981) based on 41 sacrificed gravid females according to the multivariate, predictive equation:

$$F = 15.479 - .437 (\text{Head } W) + .204 (\text{Mass}) - 1.957 (\text{Tail } F) + .657 (\text{Thigh } F)$$

where F = predicted fitness (number of eggs). The model is significant at $p = .001$ with $R^2 = .61$. The regression was applied to the treatment and control females of both years.

For male fitness, I linked male consort observations with female fecundity to weigh each male's fitness with that of his consorts. Consorts are defined in this study as lizards of the opposite sex that were observed with or ≤ 20 m from a given individual. The time a given male spent with a given female was weighted in proportion to that

female's total time with all males as follows:

$$F_m = \sum_{f=1}^n P_{mf} F_f$$

where F = fitness, m = individual male, f = individual female and P_{mf} = proportion of female f 's time spent with male m . This index combines spatial proximity with temporal overlap to estimate male reproductive fitness and assumes a proportional allotment of a female's eggs to her consorts. Eggs were assigned to males on the basis of each male's opportunity for investment in a given female's clutch. While some females do produce more than one clutch a season I could not determine which females did. The relationship between body size, seasonal conditions and multiple clutching is poorly understood. I observed large females that probably produced only one clutch and smaller females who produced at least two in the same season. In this experiment I am concerned with relative fitness among individuals over the experimental interval only and so make the simplifying assumption that all mature females reproduce only once each season. Note that the fitnesses of both sexes may be halved to reflect actual genic contributions to each egg (offspring). Such a transformation by division would not, however, affect the relative contribution among individuals and so was not performed.

RESULTS AND DISCUSSION

Fitness

Darwinian prediction holds that disparate fitnesses will accrue between the sexes and that males, the sex with least investment per gamete, will have the greatest variance in fitness. This study found

male variances were significantly higher than female, in all sites and seasons (Table 1). In all cases standard deviations were more than three times greater for males than for females. The magnitude of the differences in variances supports two additional hypotheses. One, that males providing mates with genetic benefits only will have a very large variance and two, that sexually dimorphic, polygamous species will experience pronounced discrepancies both between the sexes and among the males.

Habitat

The enclosed site was altered to eliminate habitat diversity and so, of course, was vegetatively quite different from the control sites. As a group, the controls were statistically separable from the treatment in terms of bare ground, grass and forbs (Table 2). The treatment had significantly more bare ground and less grass and forbs than the control sites. Shannon-Wiener diversity indices were calculated over the three vegetation categories for each perch at each study site. Collectively, the control sites were significantly more diverse in habitat than the treatment (Table 2). Prey items were equally abundant on all sites (Table 2). I tested the habitat variables in Table 2 for relationships with fitness. The sole significant correlation was a positive one between fitness of control males and habitat diversity (Figure 3).

Diversity of perch use by individuals reflects both the number of perches used and their relative frequency of use. Treatment males had greater perch use diversities than females (U-test, $n_1 = 10$, $n_2 = 13$, $U = 22.5$, $p = .05$) (Figure 4). No such difference between sexes was seen for control males. To relate perch use diversity to habitat, I calculated a mean habitat diversity weighted by perches used by

individuals. This combined habitat diversity with an individual's perch preference. I found no differences between the sexes in this variable nor correlations with fitness.

Darwinian theory holds that territories somehow serve to increase fitness. Despite the common assertion that collared lizards are a territorial and polygamous species, I found little direct relationship between male territories and their fitnesses. The only significant link between territory features and fitness was one between control males and habitat diversity. Because males do not directly provision females with material resources from territories, and because female territories are largely exclusive of males (Yedlin and Ferguson 1973) it is difficult to interpret the male correlation. On the one hand habitat diversity may directly and positively promote male fitness. On the other hand habitat diversity may not be a direct determinant of male fitness, but rather an artifact of attempts by males to hold territories containing perch overlaps with as many female territories as possible. This would promote diversity of male territories and correlation with male fitness, but the relationship would be a proximate side-effect and not an ultimate selective factor.

Similarly, the difference in perch use diversity between the sexes may be interpreted in different ways. Males may use more perches more often than females because males are more active (see Behavior Results). Alternatively, the significant differences between the sexes may be an artifact of the regularly spaced perches (rock piles) in the treatment site. Perches are more numerous and close together than in the control sites, and treatment males by default may use more perches per area than males in the control sites, though both groups are equally active.

Females in both groups are more sedentary and less likely to contact many different perches. Perch use diversity of males and females in the control sites may not be different because of the limited number of perches available: both sexes use the few available perches equally. Males move about more but do not encounter significantly more perches. In the treatment, males encounter more perches because there are more perches available within short distances of one another. I did not find home range size to differ between the sexes, so males, more actively using an area equal to that of females, are likely to use more perches if the perches are closely spaced.

Test of Habitat versus Male Quality Effects on Fitness

I combined the 1982 treatment and control site males in a test of the relative influences of habitat (or territory) quality and male quality on fitness. Because the control males obtain their reproductive fitnesses in heterogeneous habitats and the treatment males in an experimentally homogeneous one, any differences in the pattern of fitnesses may reflect an environmental influence.

I tested the null hypothesis that the pattern of male fitnesses in heterogeneous habitat is equivalent to the pattern of male fitnesses in homogeneous habitat. If habitat does not influence male fitness I would expect a morphological regression model to explain equally the variation in fitness of both treatment and control males. Alternatively, if habitat does influence fitness, a morphological model alone would be less adequate for control males. I tested the relative precision of the multiple regression with residual analysis, which measures the extent to which the model fails to fit the data.

A multivariate model of male fitness as a function of morphology

was constructed from both treatment and control males pooled. Two independent variables (SVL and Mass) were included; additional morphological variables did not significantly improve the regression.

The model is:

$$F = -62.258 + .876 (\text{SVL}) - .487 (\text{Mass})$$

with $n = 22$, $R^2 = .37$ and $p = .012$.

I separated the treatment and control males and tested for differences in residuals between the two groups. The test was not significant (t-test, $t = -.803$, $p = .431$) and the null hypothesis was not rejected. The pattern of variation of fitness among the control and treatment males was equally explained by the two size variables, SVL and Mass.

As an additional test for influence of habitat on observed fitness of control males I applied the pooled male model (above) to the control males only and then added to the model the variables of habitat diversity, perch use diversity, home range size and mean amounts of bare ground, grass and forbs. If habitat features are important predictors of fitness in variable environments, I would expect improved explanation of the variance of fitness when habitat variables are added to the morphological variables. The test was not significant; the fit of the morphological model was not significantly improved by the addition of habitat variables.

These tests do not preclude habitat influences, as high quality males may either select for or be the result of high quality habitats. However, I found no correlations between morphology and habitat diversity or amounts of bare ground, grass or forbs. It is of course possible other variables of habitat quality are important but were not

measured in this study.

Morphology

The sexes showed significant differences in morphology (Table 3). For all sites, males had greater mean snout-vent lengths, tail lengths, gapes, head widths and tail widths. The treatment males for both years displayed a greater mean mass. Thus larger size in addition to brighter coloration and different body proportions contributes to the sexual dimorphism of collared lizards.

Morphological variables were highly interrelated within a sex (Tables 4 and 5). Many authors have observed the significant relationships between behavior, fitness and morphology. Larger values for morphological traits are powerful predictors of aggressive success (Rand 1967, Berry 1974, Ruby 1978, 1981, Stamps 1978, Fox and Rostker 1982) and of clutch size (Martin 1977, Ruby 1981) in many different lizard species.

I showed earlier that females may select males on the basis of intrinsic quality irrespective of territory. Morphology, then, is expected to be important in conferring fitness. I used multiple regression and bivariate correlations to test morphological variables for their predictive value in relationship to fitness. The best model of fitness for all 1982 males (pooled control sites and treatment) incorporated the variables SVL, tail width, thigh fat, gape and mass (Table 6). Standardized coefficients, which serve to rank dependent variables by their predictive importance in the model, since all variables are transformed to an equivalent scale, revealed that SVL was the most important variable. Tail width, was also important, though at less than one-half the level of SVL. Tail width, like SVL, can be

considered indicative of size in that it reflects the stoutness of the tail base. Males with large body lengths and thick tails are very likely to show high fitness. As a separate indication of the importance of size, SVL was significantly correlated with fitness ($n = 22, r = .31, p = .03$). The other three variables in the multiple regression, thigh fat, gape and mass, have negative signs associated with their coefficients. This is most likely due to the high degree of intercorrelation among the morphological variables (Table 4). Variables that correlate positively with each other often acquire coefficients with opposite signs in multiple regression. When some variables are less than perfectly intercorrelated there is some variation in one variable not associated with the other variable. This variation may additionally influence the dependent variable, and it may be opposite to the effect of the intercorrelated variable. This makes direct interpretation of the coefficients and their signs difficult. Thus, due to correlation between gape and SVL for example, given that SVL is in the model, gape explains only a small portion of the pattern of fitness and with a negative effect. Similarly, the negative signs for thigh fat and mass may reflect strong intercorrelation among the independent variables (Table 4). Alternatively, it is possible that males lose mass during the reproductive season, and that fitter males (larger SVL) have proportionately low body mass and fat stores in the thighs. In any case, it appears that body size (as measured by SVL) is the single most important morphological variable that predicts the fitness of males.

I also tested females for the relationship between morphology and fitness. Female fitness was predicted from morphology of 41 sacrificed

females and their egg counts (see Fitness Methods). I examined the standardized coefficients of the variables in the fitness model and found mass the most predictive (Table 6). Head width was next important, and negative, probably due to its intercorrelation with mass (Table 5). Thigh fat was marginally important, with tail fat highly intercorrelated with thigh fat and thus acquiring a negative sign. Mass, in addition to being the most predictive of the morphological variables in the multiple regression, was significantly correlated with fitness for the control and treatment females ($n = 30, r = .64, p = .001$). Mass has been questioned as an appropriate index to size and fecundity (Dunham 1978, but see Wright 1968) due to the variation of stomach contents and eggs in subjects as they are weighed. I partially corrected for this by the subtraction of .5 g for each food bolus palpated. It is apparent that morphology is a powerful predictor of fitness for both males and females. Increasing size is positively associated with fitness for both sexes. SVL is the best measure of size and predictor of fitness for males and mass is the best for females. SVL of males and mass of females are used below to examine relationships between individuals, their consorts and fitness (see Fitness and Consorts).

Behavior

In 1981, observations of treatment lizards were emphasized with detailed behavioral data recorded in 10-minute intervals. Since in 1982 the study included three control sites in addition to the enclosed site, more census data were collected and fewer detailed observations made. I compared the relative percent of total observations for each of the 11 behaviors between years in the enclosure and found no differences

(U-tests, $n_1 = 9$, $n_2 = 23$, $p > .05$ for all tests). Similarly, no differences were found between treatment and control lizard behaviors (U-tests, $n_1 = 24$, $n_2 = 32$, $p > .05$ for all tests). Subjects of different sites and seasons were therefore pooled for this analysis of behavior.

Males were more active than females (Table 7). Males showed greater variability for chase, fight, display, mount and courtship behaviors. Females had greater variances for bask, alert bask, alert, forage, aggression and maintenance behaviors. These differences between and among the sexes are in accordance with predictions about sexually dimorphic, polygamous species. Males, more variable in fitness than females (Table 1), are also more variable in behaviors that relate to fitness: aggressive and courting actions. Females, under different selective pressures than those of males, are more variable in body maintenance behaviors. The high variability for maintenance behaviors among females may be due to intrasexual selection favoring female inactivity when certain requirements of mates, habitat and body size/condition are met. Females deficient in one or more of these categories (small females with small mates, for example) may be more active and aggressive and spend less time basking and foraging than other females.

Behavioral variables were examined for their predictive relationship to fitness. Key behaviors, similar to key measures of size, were identified. Multivariate tests were not appropriate for identification of key behaviors due to the multiplicity of similar values, including zeros, among the variables. Instead, I designated the four suites of aggression, courtship, maintenance and activity as key

behaviors and used them to test the relationships between individuals, their consorts and fitness (see Fitness and Consorts).

Other types of activity were examined for relationships to fitness. I measured sexual activity from observations of individuals with consorts. I computed total number of observations of an individual with members of the opposite sex ('Sightings with Consorts'), total number of different individuals of the opposite sex with which an individual was ever observed ('Number of Consorts'), the ratio of 'Sightings with Consorts' to 'Total Recaptures' ('Popularity') and the ratio of 'Number of Consorts' to 'Sightings with Consorts' ('Promiscuity'). I calculated mean recapture radii (Tinkle 1967) as an index to home range size for each lizard. I examined correlations of the sexual variables with total recaptures over the season, home range size and fitness (Table 8).

Fitness of males was positively correlated with 'Sightings with Consorts', 'Number of Consorts' and 'Total Recaptures'. This was in part expected, as a male's fitness was computed from his proportional allotment of eggs from consorts as estimated from his frequency of occurrence with individual females.

Individuals not often with the same consort (high 'Promiscuity' scores) had large home ranges and low scores for 'Sightings with Consorts'. 'Promiscuity' scores in both sexes were correlated positively with 'Home Range Size' and negatively with 'Sightings with Consorts' and 'Total Recaptures'. This suggests that individuals who move about a good deal spend less time with specific consorts. Because females were less active and used fewer perches than males (Figure 4), males frequently consorting with only a few different females (smaller scores for 'Number of Consorts') were also found on fewer perches than

males not often with the same consort. Consorting pairs were almost always on perches, and because it was easier to observe lizards on perches than in the grass patches, number of observations ('Total Recaptures') may be biased toward the more sexually active individuals. That 'Promiscuity' is negatively correlated with 'Total Recaptures' also indicates that highly promiscuous individuals are not often on perches or regularly with consorts. As an alternative explanation, the negative correlation between 'Promiscuity' and 'Sightings with Consorts' is somewhat artificial. Inasmuch as 'Promiscuity' is a ratio with 'Sightings with Consorts' as the denominator, one would expect a negative correlation between the denominator and the ratio.

Females showed a negative correlation between 'Total Recaptures' and 'Popularity'. On the one hand this may be due to the fact that 'Total Recaptures' is the denominator of the ratio 'Popularity'. On the other hand the correlation may be biologically relevant because females, somewhat more sedentary than males, were often on perches even when not consorting. Score differences among individual females for the two variables of the correlation may reflect the high variance among females for maintenance behaviors. It appears the more popular females had fewer recaptures and performed fewer maintenance behaviors (typically done on perches) than did the other, less popular females.

Summarizing general behavior patterns, certain individuals within each sex exhibited fewer aggressive and courting behaviors than did the others. Both sexes were separable into high and low scoring groups for most of the sexual behaviors. Promiscuous individuals appeared behaviorally distinct from less social lizards. Below I incorporate these two general patterns of behavior into a theory of alternative

mating strategies among these lizards.

Fitness and Consort-Groups

An individual's fitness is in large part dependent upon consort characteristics. For males--in addition to the obvious influence of number of consorts--size, behavior and fecundity of consorts may affect fitness. Females, while more restricted in their maximum number of offspring, may still enhance their reproductive fitnesses through mate choice based upon heritable qualities in males and/or material benefits to themselves or offspring. Consort variations in morphology and behavior may serve as clues to mating preferences and strategies. Many authors have noted the positive relationships between large size and mating opportunities for males, and fecundity for females. This study shows a relationship between size and fitness for both males and females. A male may realize high fitness through consorting with many females of mediocre fecundity, or with a few, very fit females. Fewer females require less guarding from other males, and also offer increased probability of paternity. While more of a male's reproductive investment is proportionately at risk in fewer mates, collared lizards are less vulnerable to predation and mortality the larger they grow (Fitch 1958). Larger females produce more eggs, and are most likely to contribute superior genotypes of large size and longevity. Larger females may find it advantageous to consort with only a few larger males, thereby reducing the risk of courtship and mating exposure with many mates, and assuring their eggs will be fertilized with genes of superior (larger, older) males.

Smaller males, confronted with reduced access to optimal females may follow alternative mating strategies. These include sneaking

fertilizations, satellite male tactics and nomadic wandering (Constantz 1975, Howard 1981, Krebs and Davies 1981). Smaller males are less likely to discriminate between mates on a size or quality basis inasmuch as smaller males have fewer mating opportunities. Smaller females probably prefer larger mates but larger females may either guard their large mates or drive away the smaller females. As a result smaller females are more likely to encounter, and mate with, smaller males.

I examined the relationships between individuals and their consorts in terms of fitness, morphology and behavior. I addressed the role of number of consorts, mean consort fitness and mean morphological and behavioral characteristics of consorts in conferring fitness to an individual associating with several members of the opposite sex. I also examined patterns within consort-groups, asking what is the relationship among size of a consort-group, the mean fitness of the group and the mean morphology and behavior of the group's members.

I computed means of fitness and selected morphological and behavioral traits for the consort-groups of each lizard. Fitnesses were computed from the size-specific fecundity model for females and the social equation for males, then averaged across all the consorts of an individual male or female. Morphological characters are consort averages of the fitness-predictive variables SVL for males and mass for females. Mean key behaviors are consort-group averages for the behavioral suites of aggression, maintenance, courtship and activity. The following results report those Kendall's correlations which were significant at $p < .05$. Table 9 summarizes the trends in correlation between individuals and the mean traits of their consort-groups. Table

10 summarizes the significant correlations within consort-groups.

Consort-group analysis provides evidence in support of two mating strategies: 1) larger individuals mate with fewer, larger consorts and 2) smaller individuals mate with many, smaller consorts. As expected, a regression of male fitness against number of consorts was positive and significant (Figure 5). Alternatively, female fitness was negatively correlated with number of consorts (Table 9). While multiple mates obviously enhanced male fitness, female fitness decreased with an increase in mates. The less fit females (smaller) consorted with more males than the larger females. Note that female fitness is independently predicted from a size-specific model, but male fitness is calculated from proportional allotment of eggs from total consorts. The regression of male fitness and number of consorts is expected to be positive and alone is not capable of distinguishing between the two mating strategies, as is the female test.

Male fitness may be as much a function of consort fecundity as numbers of consorts. Indeed, mean fitness of female consorts was positively correlated with male fitness (Table 9). I made a direct test of the hypothesis that males with few consorts will have consorts with greater mean fitness than males with many, but on the average less fit, consorts. The pooled control and treatment males were divided in half on the basis of numbers of consorts. I tested for differences in mean female (consort) fitness between the two groups. The test was significant: males with fewer consorts had consorts with greater average fitness than males with many consorts (one-tailed t-test, $n = 18$, $p < .05$). This constitutes further support for two mating strategies among males.

As shown earlier, mass was a significant indicator of female fecundity, and mean mass (like mean fitness) was positively correlated with male fitness (Table 9). Also, the male measure of size, SVL, was positively associated with fitness of female consorts. This suggests both larger males and females selectively consort with more fecund (larger) mates. Mean mass of females was negatively correlated with consort-group size and consort-group size was also negatively correlated with mean fitness of consort-group males (Table 10). Thus smaller females were found in the large consort-groups and larger (fitter) males were in the small consort-groups.

These two strategies are also supported by the negative correlations between mean courtship and SVL of males in consort-groups (Table 10). Fitter males (as indexed by SVL) spend less time courting and more time in activity (Table 10). This suggests larger males are engaged in activities other than courtship, and that smaller males engage in courtship significantly more often than larger males. Larger males spend their time consorting with a few large females and possibly actively sequestering them from other males. These large females may be similarly engaged in monopolizing the large males and repelling other females and smaller males. Females with larger mates tend to be large themselves, and probably do not need to express aggression towards smaller females. Instead smaller females most likely avoid the larger females. Female aggression decreases with size of male consorts (indexed by mean SVL of males) and with mean activity of male consorts (Table 9). Female aggression increases with increased number of consorts (Table 9). Smaller females are differentially subjected to more courtship, from smaller males, than are larger females. Smaller

females, who have more consorts than do large females, may be aggressive to both smaller, undesirable males and to larger females who are restricting access to large males.

These results may also be evidence of a strategy to differentially increase a female's fitness by hoarding superior male sperm (i.e not permitting other females access to the male) even when the female cannot make complete use of the male's supply. This is a female parallel to the super-territory hypothesis by Verner, 1977. Verner suggested males may differentially improve their relative fitness by monopolizing more resources than strictly needed for reproduction in order to make the resources unavailable to other males. The other males suffer reduced reproductive success, and as a consequence, the super-territory holder's fitness is relatively improved. The super-territory hypothesis has been variously criticized, notably because the benefits of having fewer males in the general vicinity of the super-territories would be enjoyed by all local males, and not just by the individual(s) holding the larger than required territories (Colgan 1979, Pleasants and Pleasants 1979). In my study, however, the positive benefits of superior male genes are enjoyed by the defending female only, and thus the strategy would be promoted by differential fitnesses and individual selection.

CONCLUSIONS

Collared lizards do behave according to some of the predictions about sexually dimorphic and polygamous species. The sexes assume roles of salesmanship and coyness. Males are more variable in fitness than females, and fewer males mate. But I also conclude collared lizards are

socially more subtle and complex than previously reported.

The sexes are territorial in very different senses from one another. It is difficult to attribute strong, direct influence to the territories of males in promoting reproductive fitness. Male collared lizards do not directly provision females with food or exclusive space for purposes such as nesting, foraging or seeking refuge. Instead, females maintain their own home ranges (if not properly territories) and have only a small degree of overlap with males (Yedlin and Ferguson 1973, Bontrager 1980, personal observation).

In several ways collared lizards approximate the well-studied iguanid species Sceloporus jarrovi. As described by Ruby (1978, 1981) and others, male S. jarrovi, in May as the non-hibernating species becomes territorial, initially hold large but not inviolate territories. Female S. jarrovi eventually settle upon smaller territories, whereupon males shift and shrink their territories in an attempt to overlap as many females as possible. The new male territories are smaller, defensible, and to a great extent apparently based upon, not male but female choice of habitat. This is significantly different from classic scenarios of male-established territories and late-arriving females selecting among males (or territories) for key genetic (or material) benefits (e.g. Weatherhead and Robertson 1977, Searcy 1979, Yasukawa 1981, Andersson 1982, Loiselle 1982).

In collared lizards, like S. jarrovi, female territories probably exert positive influence on fitness through the traditional provision of food, cover and nesting sites. Female collared lizards appear to select their material resources directly, early in the reproductive season, before males are sexually active (Fitch 1956, personal observation).

This exercise of female choice appears to be followed by male courtship of females. Which females they court is probably determined by some combination of territory quality, female quality (size probably) and spatial distribution of females. In turn, females, secure on their independent territories, may rely upon male intrasexual selection (competition) to provide genetically superior males on their doorsteps with which to mate.

These variations on simple mate choice enlarge the possible role of mate choice by males. At least some males, like females, practice mate choice strategies (e.g. Wade and Arnold 1980, for theoretical models, Loiselle 1982, on pupfish). Sperm is not free, neither is the time necessary to locate, court and mate with a female. Predation risks are indisputably high during courtship and possibly maximal during copulation. Even assuming the courtship-copulation process is relatively inexpensive, a male ought to mate with as fit a female as he can get (find, hold, defend). Given the simplest of choices, i.e. between two females, the adapted male should select the one promising the best return for his efforts. In even the simplest dichotomous choice where the two equally available females are not exactly equivalent in terms of fecundity, health, age, material benefits, etc., the male will benefit by selecting to mate first with the superior female. If, following that mating, he may service the second, so much the better. If, during the time he is mating with the first, another male spirits away the second female, at least the male invested wisely in the superior mate in the context of available mating opportunities.

As suggested above, high male fitness may be obtained through indiscriminant mating with many females or through discriminant pairing

with only high quality females. It is not uncommon to find alternate mating tactics in a population (e.g. Constantz 1975, on fish, Howard 1981, on frogs, Waltz 1982, on invertebrates and vertebrates). To some extent an individual may facultatively switch strategies, or combine them, or move from one strategy to the other as it grows older and larger. The two mating strategies among collared lizards which I defined may be endpoints of an ontogenetic continuum of strategies. Individuals, as they grow older (hence, larger), may move along this continuum from many, small mates to few, large ones.

Decisions to invest time and energy in a given pairing may be similar to optimal foraging models where search, pursuit, capture and ingestion costs and success probabilities are assessed in varying environmental contexts. Applied here, a male must decide to court or not, and so on, based upon his expectation of success in obtaining the mating cheaply enough to be worthwhile and his expectation of obtaining a superior mate in the same time-cost framework. The economics of the decision are different for larger and smaller individuals and thus two mating strategies are employed.

The presence of alternative mating tactics, coupled with the economics of different tactics sets up a conflict between the sexes. I have shown that large females consort with few large males and vice versa. However, there is a tendency for all males, regardless of size, to try to mate with as many females as possible. Females want few, but the best males, whereas males want more consorts, always. This increases their fitness (Figure 5). Larger males have the luxury of obtaining large females but larger males probably are also interested in available "inexpensive" smaller females as well. However, larger males

are "controlled" by their few, large female consorts. Large females monopolize the large males (sensu super-territories) and keep small females away. This results in large males having fewer consorts, but because they are fitter consorts it does not prove beneficial for the large males to leave their large females in search of more mates at some distance away. Collared lizards perform stereotypic courtship behavior, and the time needed for the requisite courting before copulation may both limit total matings for a male and discourage males from seeking additional females. Timing of ovulation and patterns of sperm receptivity may also favor male fidelity. While details of sperm competition are poorly known for most reptiles (but see Parker 1970 on insects, Arnold 1976 on salamanders and Cheng, Burns and McKinney 1983 on ducks) it is likely that timing and sequence of copulation influences the success probabilities of sperm. Depending on which insemination is most likely to fertilize eggs, males may find it beneficial to guard females, at least at certain times, from promiscuous matings with other males. In a sense, the best males are "satisfied captives" of the best females. In the conflict between the sexes females seem to be in control.

The strategy of larger males to select high quality females gives a new importance to habitat (territory) quality. I showed experimentally that females are capable of, and in practice do, select mates based upon intrinsic qualities regardless of habitat when I found similar patterns of fitness among the treatment and control males. I concluded female territories are directly selected by females and directly promote fitness. Male territories are extended overlaps with females, and are probably proximate effects of male intrasexual competition for mate

access. Some males may not directly choose their territories but instead choose females already on territories. In making reproductive decisions males may use territory quality along with intrinsic quality as indicators of which females to court.

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Table 1. Differential variances of fitnesses between male and female Crotaphytus collaris, 1981-1982. Control sites are pooled.

| Site | Year | N | Male | | Female | | F | p |
|-----------|------|----|----------------------------|----|----------------------------|-------|------|---|
| | | | $\bar{X} \pm 1 \text{ SD}$ | N | $\bar{X} \pm 1 \text{ SD}$ | | | |
| Treatment | 1981 | 4 | 8.97 \pm 7.06 | 5 | 7.16 \pm 1.67 | 17.77 | .01 | |
| Treatment | 1982 | 10 | 6.42 \pm 4.93 | 13 | 5.10 \pm 1.54 | 10.30 | .001 | |
| Control | 1982 | 12 | 4.04 \pm 4.51 | 12 | 5.37 \pm 1.37 | 10.86 | .001 | |

Table 2. Differences in habitat variables between treatment and pooled control sites, 1982. Means calculated over all perches (n = 35 for treatment, n = 27 for controls) and given in m of bare ground, grass and forbs per 12 m of summed transects, mean H' for Shannon-Wiener diversity indices and prey density for mean prey counts per sampling effort.

| Variable | Treatment \bar{X} | Control \bar{X} | U |
|--------------|---------------------|-------------------|---------|
| Bare ground | 40.00 | 20.76 | 67.0* |
| Grass | 0.00 | 1.82 | 69.0* |
| Forbs | 0.00 | 17.42 | 73.0* |
| H' | 0.00 | .49 | 52.5* |
| Prey density | 11.00 | 10.00 | 31.0 NS |

* $p < .05$, Mann-Whitney U-test.

Table 3. Morphological differences between sexes of Crotaphytus collaris.

Treatment lizards combined for 1981-1982, control sites pooled. Treatment male n = 14, treatment female n = 18, control male n = 12, control female n = 16.

| Site | Variable | Male | Female | t° | p° |
|-----------|----------|----------------------------|----------------------------|------|------|
| | | $\bar{X} \pm 1 \text{ SD}$ | $\bar{X} \pm 1 \text{ SD}$ | | |
| Treatment | SVL | 100.29 \pm 8.79 | 89.00 \pm 7.07 | 4.03 | .001 |
| | Tail L | 187.64 \pm 24.72 | 163.67 \pm 11.93 | 3.34 | .004 |
| | Gape | 24.14 \pm 2.28 | 18.67 \pm 1.37 | 7.93 | .001 |
| | Head W | 26.64 \pm 2.59 | 20.33 \pm 1.38 | 8.50 | .001 |
| | Tail W | 12.64 \pm 1.08 | 9.94 \pm 1.55 | 5.54 | .001 |
| | Mass | 39.25 \pm 10.49 | 28.29 \pm 6.62 | 3.58 | .001 |
| Control | SVL | 92.00 \pm 5.39 | 86.69 \pm 5.51 | 2.55 | .017 |
| | Tail L | 185.58 \pm 11.95 | 163.31 \pm 9.79 | 5.42 | .001 |
| | Gape | 22.42 \pm 1.31 | 18.62 \pm .96 | 8.86 | .001 |
| | Head W | 24.25 \pm 1.71 | 20.25 \pm 1.12 | 7.46 | .001 |
| | Tail W | 11.92 \pm 1.16 | 10.44 \pm .81 | 3.96 | .001 |

° t-test statistic and associated probability.

Table 4. Kendall's correlation coefficients between morphological variables for male Crotaphytus collaris, 1981-1982. All sites pooled over both years. N = 26.

| | SVL | Tail L | Gape | Head W | Tail W | Mass | Tail Fat | Thigh Fat | Color | Femorals |
|-----------|------|--------|------|--------|--------|------|----------|-----------|-------|----------|
| SVL | 1.00 | .58* | .73* | .77* | .52* | .83* | -.07 | -.07 | .42* | .51* |
| Tail L | | 1.00 | .50* | .56* | .34* | .56* | -.10 | -.06 | .23 | .28 |
| Gape | | | 1.00 | .78* | .57* | .69* | -.16 | .01 | .54* | .63* |
| Head W | | | | 1.00 | .54* | .79* | -.06 | .01 | .49* | .56* |
| Tail W | | | | | 1.00 | .53* | .20 | .21 | .43* | .39* |
| Mass | | | | | | 1.00 | .011 | .05 | .37* | .47* |
| Tail Fat | | | | | | | 1.00 | .40* | -.02 | -.16 |
| Thigh Fat | | | | | | | | 1.00 | .21 | .23 |
| Color | | | | | | | | | 1.00 | .69* |
| Femorals | | | | | | | | | | 1.00 |

* p < .05.

Table 5. Kendall's correlation coefficients between morphological variables for female Crotaphytus collaris, 1981-1982. All sites pooled over both years. N = 30.

| | SVL | Tail L | Gape | Head W | Tail W | Mass | Tail Fat | Thigh Fat | Color |
|-----------|------|--------|------|--------|--------|------|----------|-----------|-------|
| SVL | 1.00 | .66* | .29* | .45* | .27 | .69* | -.32* | .10 | .32* |
| Tail L | | 1.00 | .50* | .52* | .44* | .53* | -.31* | .04 | .09 |
| Gape | | | 1.00 | .65* | .58* | .26 | .15 | -.06 | .11 |
| Head W | | | | 1.00 | .46* | .33* | -.29 | -.16 | .03 |
| Tail W | | | | | 1.00 | .35* | .05 | .03 | .01 |
| Mass | | | | | | 1.00 | -.13 | .09 | .37* |
| Tail Fat | | | | | | | 1.00 | .36* | .05 |
| Thigh Fat | | | | | | | | 1.00 | .15 |
| Color | | | | | | | | | 1.00 |

* $p < .05$.

Table 6. Importance of morphological variables in predicting fitness of male and female Crotaphytus collaris from multiple regression. Male n = 22, female n = 41.

| Males | | | Females | | |
|--------------------------------------|--------------------------|-----------------------|--|--------------------------|-----------------------|
| R ² = .51 F = 3.4 p = .03 | | | R ² = .61 F = 14.3 p = .001 | | |
| Variable | Standardized Coefficient | % Relative Importance | Variable | Standardized Coefficient | % Relative Importance |
| SVL | 1.400 | 37.9 | Mass | 1.125 | 57.7 |
| Mass | -.967 | 26.2 | Head width | -.424 | 21.7 |
| Tail width | .590 | 16.0 | Thigh fat | .212 | 10.9 |
| Gape | -.511 | 13.8 | Tail fat | -.188 | 9.7 |
| Thigh fat | -.227 | 6.1 | | | |

Table 7. Between sexes differences in behavior of Crotaphytus collaris, 1981-1982. Sexes are pooled over sites and years. Values are mean percentages of total observations. Male n = 26. female n = 30.

| Behavior | Male | Female | F |
|-------------|----------------------------|----------------------------|--------------------|
| | $\bar{X} \pm 1 \text{ SD}$ | $\bar{X} \pm 1 \text{ SD}$ | |
| Bask | 6.00 \pm 4.00 | 7.80 \pm 6.14 | 2.36* |
| Alert Bask | 34.50 \pm 4.20 | 45.60 \pm 22.40 | 28.40* |
| Alert | 24.25 \pm 10.21 | 25.20 \pm 18.06 | 3.13* |
| Active | 18.25 \pm 5.74 | 6.60 \pm 2.19 | 6.86* ^o |
| Forage | 2.00 \pm 1.83 | 3.40 \pm 3.36 | 3.39* |
| Patrol | .25 \pm .50 | .20 \pm .45 | 1.25 NS |
| Display | 8.25 \pm 7.36 | 4.60 \pm 4.93 | 2.23* |
| Chase | 2.25 \pm 3.20 | .20 \pm .45 | 51.25* |
| Fight | 2.80 \pm 5.72 | .25 \pm .50 | 130.80* |
| Touch | 3.00 \pm 3.46 | 3.40 \pm 2.70 | 1.64 NS |
| Mount | .50 \pm 1.00 | .20 \pm .45 | 5.00* |
| Aggression | 11.00 \pm 6.06 | 7.80 \pm 10.35 | 2.92* |
| Maintenance | 42.50 \pm 1.73 | 56.80 \pm 23.72 | 187.57* |
| Courtship | 3.75 \pm 4.50 | 3.80 \pm 2.86 | 2.47* |
| Activity | 77.25 \pm 12.66 | 77.60 \pm 11.33 | 1.25 NS |

* p < .05.

^o F-ratio computed as squared coefficient of variation since means were significantly different in adjusted t-test.

Table 8. Significant Kendall's correlation coefficients for sexual behaviors of treatment male and female Crotaphytus collaris, 1981-1982. Years are pooled, with male coefficients given above diagonal and female below. Male n = 14, female n = 18.

| | Fitness | Sightings with Consorts | Number of Consorts | Popular- ity [†] | Promis- cuity [°] | Home Range Radius | Total Recaptures |
|-------------------------------|---------|-------------------------------|--------------------------|------------------------------|-------------------------------|-------------------------|---------------------|
| Fitness | | .67* | .45* | - | - | - | .55* |
| Sightings with Consorts | - | | - | - | -.64* | - | .71* |
| Number of Consorts | - | - | | - | - | - | - |
| Popularity [†] | - | - | - | | - | - | - |
| Promiscuity [°] | - | -.69* | - | - | | .76* | -.54* |
| Home Range Radius | - | - | - | - | .58* | | - |
| Total Recaptures | - | - | - | -.45* | -.55* | - | |

* $p \leq .05$.

† Ratio of Sightings with Consorts/Total Recaptures.

° Ratio of Number of Consorts/Sightings with Consorts.

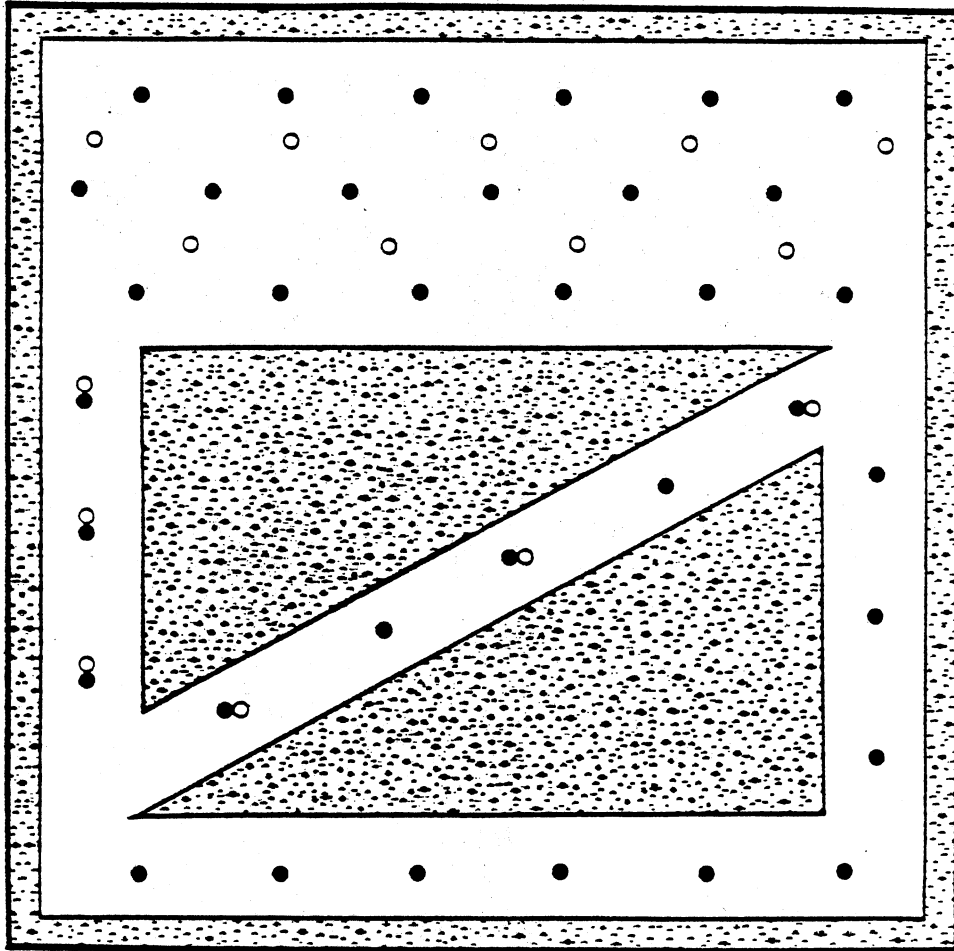
Table 9. Summary of signs of significant Crotaphytus collaris correlations between individuals and their consorts, 1981-1982. Correlations are between individuals and consort trait means.

| Consort Group Trait | <u>Consorting Male</u> | | <u>Consorting Female</u> | |
|---------------------------|------------------------|-----|--------------------------|------------|
| | Fitness | SVL | Fitness | Aggression |
| Group Size | + | | - | + |
| \bar{X} Fitness | + | + | | |
| \bar{X} Mass | + | | | |
| \bar{X} SVL | | | | - |
| \bar{X} Courtship | | | | + |
| \bar{X} Activity | | | | - |

Table 10. Summary of signs of significant correlations of trait means within consort-groups of Crotaphytus collaris, 1981-1982. Group size is the number of consorts.

| Consort Group | Male Means | | Female Means | | | | |
|-----------------------|------------|-----|--------------|------|------------|-------------|----------|
| | Fitness | SVL | Fitness | Mass | Aggression | Maintenance | Activity |
| Group Size | - | - | - | - | - | - | - |
| \bar{X} Aggression | | | | + | | | |
| \bar{X} Maintenance | | | | - | | | - |
| \bar{X} Courtship | | - | | | | | |
| \bar{X} Activity | | + | - | | - | | |

Figure 1. Plan of treatment site, 1981-1982.



Grass 

Dirt 

○ = 1981 Rockpiles

● = 1982 Rockpiles



Rockpile



Figure 2. Behaviors of Crotaphytus collaris. a = bask; b = forage;
c = display, fight; d = chase, patrol; e = alert bask; f = alert; g =
active; h = mount; i = touch.

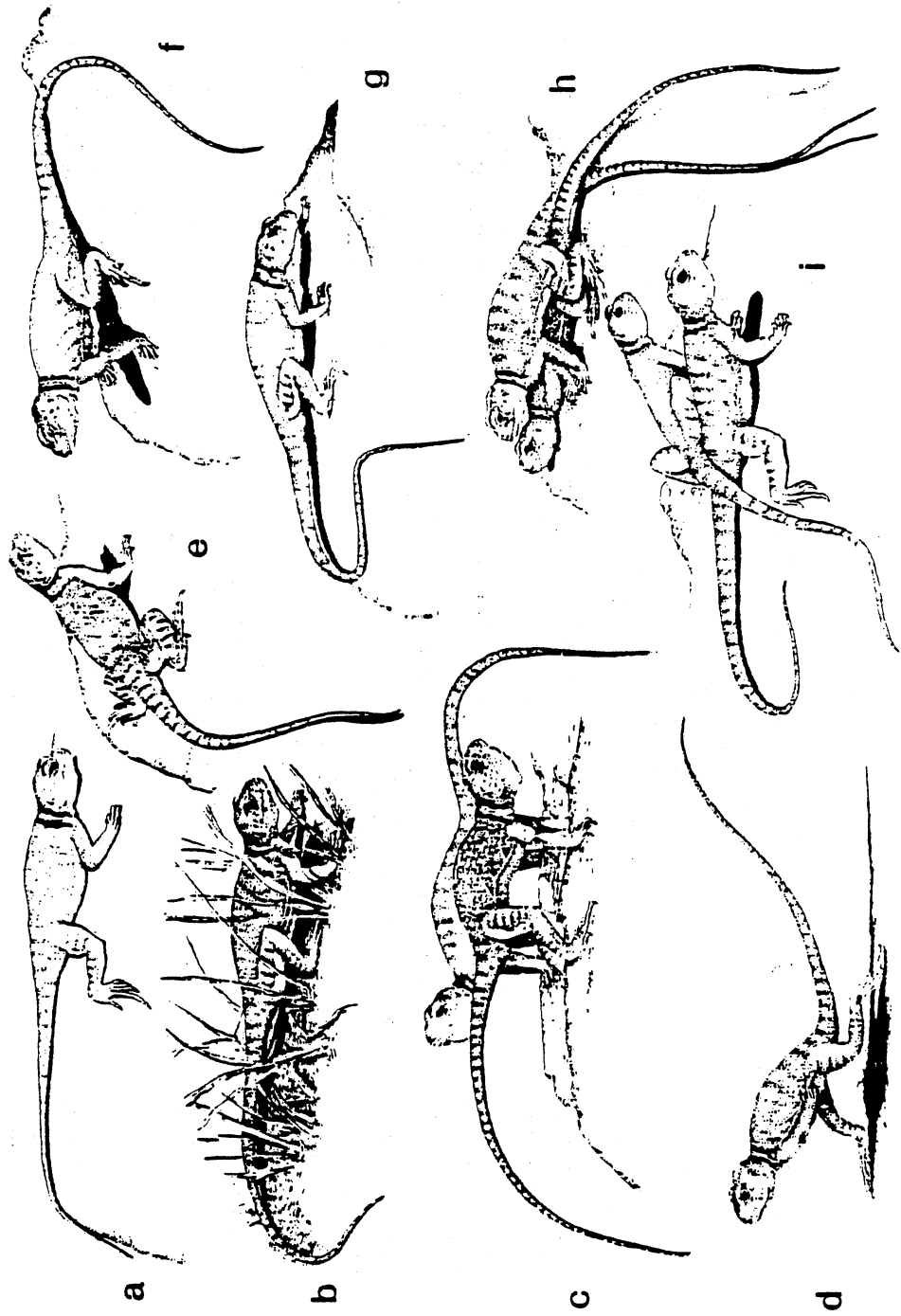


Figure 3. Fitness of control males against habitat diversity, 1982.

N = 12.

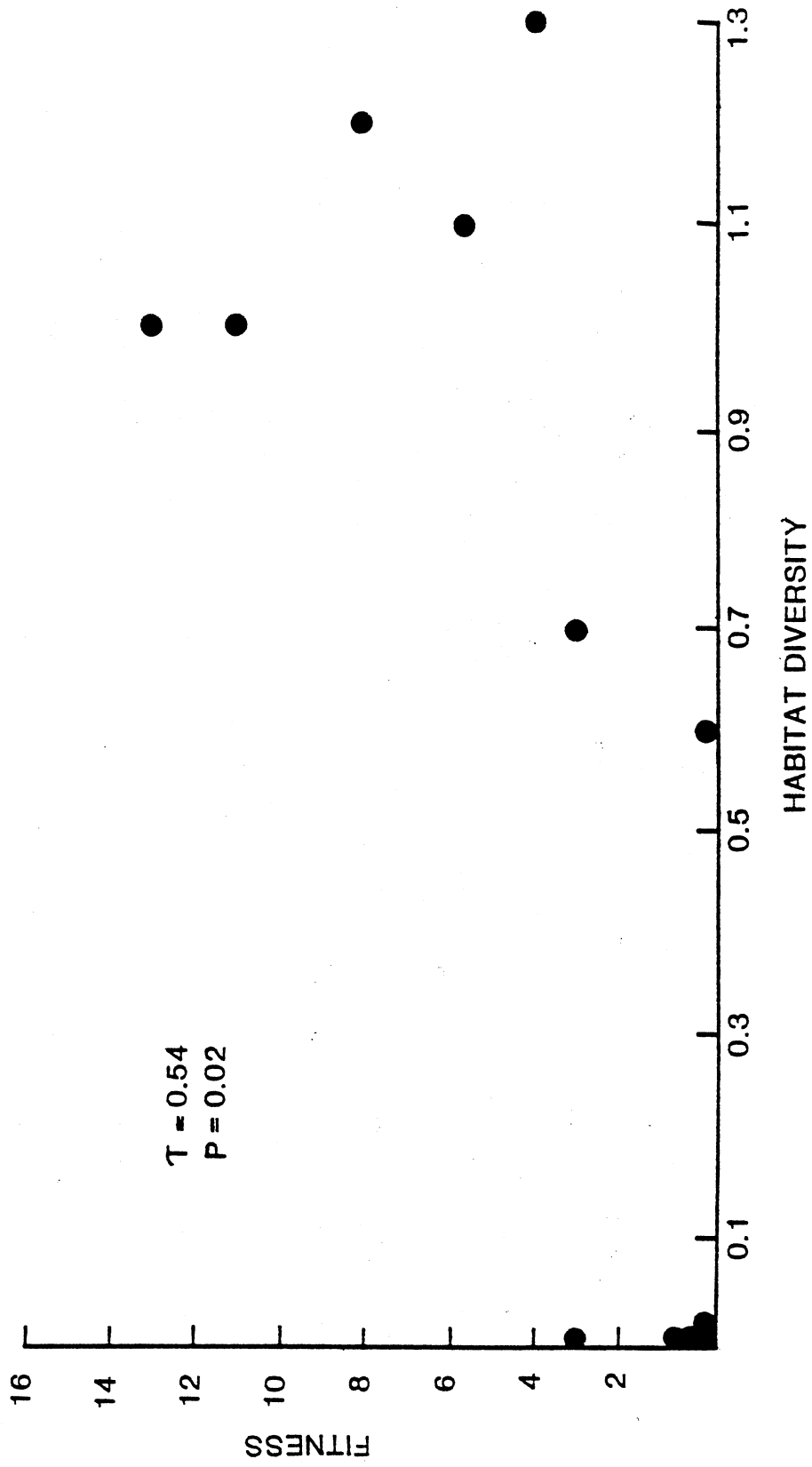


Figure 4. Differences between the sexes of treatment Crotaphytus collaris for perch use diversity, 1982. Male n = 10, female n = 13.

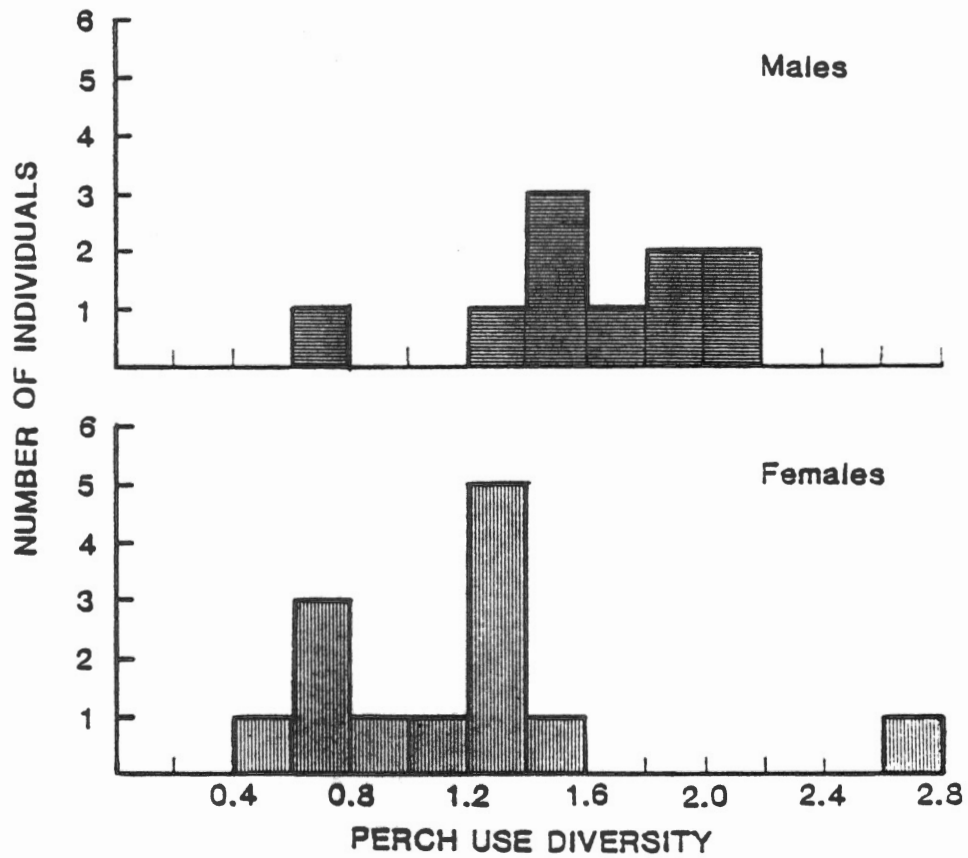
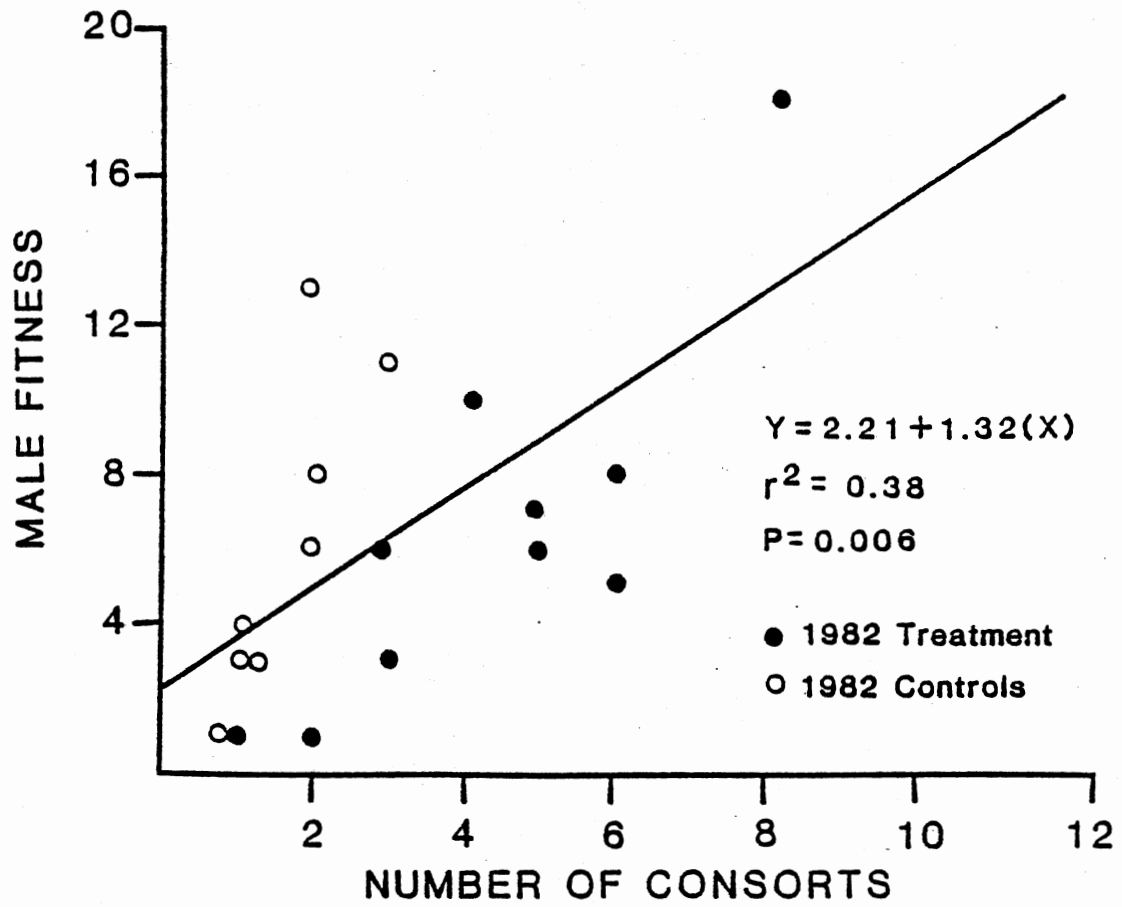


Figure 5. Least squares linear regression of male Crotaphytus collaris fitness against number of consorts. Treatment male n = 10, control male n = 12.



VITA ²

Margaret Anne Rostker

Candidate for the Degree of

Doctor of Philosophy

Thesis: AN EXPERIMENTAL STUDY OF COLLARED LIZARDS: EFFECTS OF
HABITAT AND MALE QUALITY ON FITNESS

Major Field: Zoology

Biographical:

Personal Data: Born September 10, 1950.

Education: Graduated from Pasadena High School, Pasadena, California, in June, 1967; attended Santa Rosa Community College, Santa Rosa, California, in 1972; attended Lewis and Clark College, Portland, Oregon, in 1973; received Associate of Science degree in Biology from Clackamas Community College, Oregon City, Oregon, in 1975; received Bachelor of Science degree in Zoology from Oregon State University, Corvallis, Oregon, in June, 1977; received Master of Science degree in Wildlife Ecology from Oregon State University, Corvallis, Oregon, in July, 1980; completed requirements for the Doctor of Philosophy degree at Oklahoma State University, Stillwater, Oklahoma, in December, 1983.

Professional Experience: Graduate Teaching Assistant, Oregon State University, 1978-1980; Graduate Teaching Assistant, Oklahoma State University, 1980-1983.