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GRADUATE COLLEGE

IGUANID MATING SYSTEMS: ECOLOGICAL CAUSES AND SEXUAL SELECTION CONSEQUENCES

A Dissertation

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in partial fulfillment of the requirements for the

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Doctor of Philosophy

By

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IGUANID MATING SYSTEMS:

ECOLOGICAL CAUSES AND

SEXUAL SELECTION CONSEQUENCES

A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

By

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Abstract

I investigated the mating systems of the iguanids *Ctenosaura similis* and *Dipsosaurus dorsalis,* with the goal of understanding the ecological factors impinging on resource use, mate monopolization, and sexual dimorphism. I also used a meta-analysis to test the hypothesis that the distribution of shelters from predators is an important ecological variable in structuring social systems in the family Iguanidae.

Temperature was relatively uniform throughout the forested habitat of *C. similis*, and burrows and food sources were highly clumped in space. In contrast, the xeric habitat of *D. dorsalis* exhibited great variation in temperature and food, with relatively even burrow distribution.

Ctenosaura similis females exhibited extremely overlapping home ranges near burrow sites; *D. dorsalis* females exhibited moderate levels of home range overlap beneath large shrubs offering cool temperatures. Males of both species capitalized on the clumped distributions of females; in *C. similis*, each burrow area was defended by a large male whose territory was surrounded by peripheral males. In *D. dorsalis*, most males defended territories that included at least one female, and the most successful males defended plants with the coolest shade temperatures. Thus, both species exhibited resource-defense polygyny (RDP), and the most spatially limiting resource (burrow sites for *C. similis* and low-temperature sites for *D. dorsalis*) had the greatest influence on the mating system. Overall degrees of polygyny and local mate competition were higher in *C. similis*.

Although both species are sexually dimorphic, *C. similis* is much more so.

Moreover, male *C. similis* that defended burrow sites had proportionately longer heads than peripheral males, suggesting stronger selection on head length than exists for *D. dorsalis*, for whom such a relationship was not found.

RDP is the commonest mating system in the family Iguanidae; also, most iguanids are ecologically tied to large, permanent shelters that are highly clumped in space. However, non-RDP systems have evolved independently in three lineages; all of these transitions occurred in taxa in which shelter has become less limiting. The nature of sexual dimorphism does not correspond closely either with mating systems or with degree of clumping of shelter.

Chapter 1. THE MATING SYSTEM OF *CTENOSAURA SIMILIS*: ECOLOGICAL CAUSES AND SEXUAL SELECTION CONSEQUENCES

ABSTRACT

Environmental factors may influence animal mating systems by determining the extent to which members of one sex can monopolize members of the other. Therefore, investigations of animal social evolution need to be made in the context of habitat requirements and resource distribution. I studied the spiny-tailed iguana, *Ctenosaura similis*, in northwestern Costa Rica to determine how resource distribution influences social evolution and resultant patterns of sexual dimorphism. *Ctenosaura similis* exhibited resource-defense polygyny based on food sources (flowering trees) and burrows, both of which were clumped in space. Behaviorally dominant males defended burrow areas and spent more time in the proximity of females; males of lower status had home ranges that included the flowering trees, and they intercepted females during their foraging movements. Courtship styles by the two male classes differed; low-rank males were more likely to attempt to grasp the female's neck early in the courtship sequence, and females were more likely to resist the courtships of low-rank males. Dominant males exhibited a higher copulation rate than low-rank males. *C. similis* is sexually dimorphic; males are larger and have longer and broader heads than females. Dominant males also have significantly longer heads than low-rank males when the effect of body size is removed. It is hypothesized that longer heads may be advantageous in the gaping contest that males engage in during territory disputes.

INTRODUCTION

Animal mating systems, the stages upon which patterns of sexual selection evolve, have come to be understood as outcomes of competition among individuals to maximize their individual reproductive success (Emlen and Oring 1977). Recent attention to mating systems and sexual selection has focused on two broad questions. First, what factors contribute to the evolution of mating systems? Second, within a given mating system, what is the mechanism of sexual selection--that is, what influences the outcome of male-male interactions and mate choice by females (Bradbury and Andersson 1987)?

In many polygynous species in which the male's contribution to female reproductive success is limited to sperm, female distribution is tied to environmental resources, males defend territories that encompass these resources and, hence, the females (resource-defense polygyny; Clutton-Brock 1989). The distribution of food (Bradbury and Vehrencamp 1977, Davies and Lundberg 1984), oviposition or nesting sites (Orians 1969, Alcock 1987), resting sites or refuges from predation (Baldi et al. 1996), or environmental thermal properties (Pleszczynska 1978, Carey 1991) lead to a clumped dispersion of females and the potential for mate monopolization by males. If female distribution is sufficiently clumped to allow the largest males to monopolize them, smaller males may adopt satellite behavior (e.g., Howard 1978, Gerhardt et al. 1987, Arak 1988). If there are alternative sources of females not monopolized by the largest males, males may adopt alternative mating strategies, including mate-finding and courtship strategies suited to different microhabitats and female receptivity levels (Alcock et al. 1977, Thornhill 1981, Rubenstein 1984, Waltz and Wolf 1984).

Although lizards show a variety of mating systems from extreme polygyny (Berry 1974, Trillmich 1983) to monogamy (Tinkle 1967, Bull 1994), as a group they possess two ecological traits that tend to canalize them toward the development of classical resource-defense polygyny: paternal care is lacking (Trivers 1972), and female home ranges are typically small and overlapping, with matings taking place on female home ranges (Trivers 1976, Stamps 1983, Smith 1985, M'Closkey et al. 1990, Hews 1993). Thus, local resource enhancement sets the stage for intense mate competition among male lizards (Hews 1993). Male-male competition, in turn, may contribute to the extreme dimorphisms in head morphology seen in many polygynous lizards, since in most species the head is an integral part of the displaying apparatus (crest scales, dewlaps, head coloration, etc.; Carpenter 1982, Cooper and Vitt 1988, Fleishman 1988) and the jaws are the primary weapons used in male-male contests (e.g., Vitt and Cooper 1985, Hews 1990, Olsson 1992). Hence, herbivorous lizard social systems offer opportunities to study the behavioral and morphological consequences of ecology at a number of different scales.

Resource distribution and use in herbivorous lizards, such as the Iguanidae (*sensu* Frost and Etheridge 1989), leads to paradoxical predictions, because on the one hand, food is spatially predictable and often clumped, which may lead to high home range overlap and potential local mate competition (Berry 1974, Krekorian 1976), while on the other hand leaves are seldom a limiting resource and, therefore, food dispersion may not in itself greatly influence the degree of home range overlap or territoriality (Carothers

1981, Rauch 1985, Rodda 1992). Additionally, the reliance on predator refuges such as burrows, which are often limiting, is more important in this group than in most insectivorous lizards (Iverson 1979, Carothers 1981, Case 1982, Dugan and Wiewandt 1982). In this study, I examined the ecological conditions underlying the mating system of the iguanid Ctenosaura similis and some of the consequences of the system for sexual selection, including the extreme levels of sexual dimorphism exhibited by this species. In C. similis, a complex mating structure with alternative male mating tactics has formed around two distinct ecological resources (burrows and food), which are differentially distributed in the environment. I examined the following questions: a) what factors govern female home ranges? b) how do males use these patterns of female movement to obtain access to mates? c) what factors contribute to the relative success rates of alternative male tactics? d) what are the correlates between the system of male-male agonistic behavior and sexual dimorphism?

METHODS

Study Site

I conducted the study in Palo Verde National Park, Guanacaste, Costa Rica (10°21'N, 85°21'W), one of the driest regions in Central America. The climate is highly seasonal, with virtually all of the annual 1000 to 1500 mm of rain falling from May through December (Coen 1983). The forest is characterized as tropical dry forest, and most of the trees are deciduous during the dry season, at which time many species produce flowers (Hartshorn 1983). Potential mammalian predators on C. similis at Palo Verde include coatis (Nasua narica), tayras (Eira barbara), jaguarundis (Felis yaguaroundi), and cougars (F. concolor) (Janzen and Wilson 1983).

From 7 January through 17 March 1992, I collected data from seven small groups of lizards within 1 km of the Organization for Tropical Studies (OTS) field station. The study period encompassed the bulk of the breeding season of C. similis, which is confined to a 2 - 3 month period early in the dry season (January - March, in northwestern Costa Rica; Fitch and Hackforth-Jones 1983). Each of the seven groups contained from four to twelve resident females distributed around a cluster of burrows or large hollow tree that provided refuge, and a variable number of attendant males. I constructed a scale map of the burrows and landmarks in each area, staking out a 10x10 m grid of flags to facilitate plotting lizard movements.

Capture, Marking, and Baseline Data Collection

I captured 58 adults with wire mesh live traps or with a landing net. These constituted the majority of adults consistently visible on the seven focal sites, and the remaining unmarked individuals were identified using unique patterns of color and/or dorsal crest condition. For each captured individual, the following morphological variables were measured (snout vent length was taken with a straight ruler; others were taken with digital calipers):

-snout vent length (SVL) to the nearest 5 mm.

-head width to the nearest 0.1 mm, at the widest point on the head.

-head length to the nearest 0.1 mm, from the anterior edge of the ear opening to the tip of the rostrum.

-head height to the nearest 0.1 mm, at the highest point of the head (typically at the same site as the head width measurement).

I marked each individual with colored 4-mm glass beads, a modification of the technique used by Rodda et al. (1988). I first passed a needle (soaked in antibiotic soap) through the skinflap directly beneath the dorsal crest in the shoulder region, then inserted the free end of a nylon monofilament line strung with three beads; a small metal crimp, clamped onto the free end of the line, kept it from pulling back through the skinflap. Rodda et al. (1988) found that bead-marked adult I. iguana showed handling effects for one to four days, after which no home range alterations due to handling were detected. Similar evaluations of other beading techniques, such as tail-beading (Fisher and Muth 1989), showed that this method is superior to toe-clipping or other more invasive methods. During processing, I strapped the lizards to a wooden restraining board using velcro straps; this prevented them from harming themselves by thrashing, and allowed safe handling and repeatable measurements. All individuals were processed immediately after capture and as quickly as possible (maximum process time 15 min). Although some individuals showed increased wariness for several days following their capture and marking, the effects were not long-term; many reappeared within minutes of release to display to other individuals or court, and one male was seen copulating within two hours of his release.

Focal Sampling

To quantify behavioral interactions, I took detailed focal samples of males, which included the following data:

Behavior Category - the type of thermoregulatory or interactive behavior. I recognized eight categories that included all behaviors observed:

Sun - generally motionless and positioned in sun.

Shade - generally motionless and positioned in the shade.

Clouds - generally motionless during overcast periods.

Move - any movement that lasts longer than three seconds.

Feed - feeding on vegetation; this category includes the short movements made as the animal feeds; e.g., walking through a patch of flowers and feeding simultaneously.

Court - courtship begins when a male approaches a female and initiates vibratory head-nodding (Distel and Veazy 1982; also equivalent to Dugan's [1982] "shudder bob"), a distinctive, low-amplitude head movement. A typical courtship includes bouts of vibratory head-nodding separated by pauses; if the pauses were shorter than 5 minutes, I recorded the entire sequence, including pauses, as courtship.

Copulation - copulation begins when the male moves his tail beneath the female's cloaca.

Interaction - includes chases, fights, and brief pauses during male-male encounters (e.g., stand-offs involving two displaying males).

Location - the individual's location on the scale map (when not moving).

Exposure - sun exposure, either in sun or in shade, for all behavior categories.

Discrete behaviors - the number of vibratory head-nod bouts, assertion headbobs (Carpenter and Ferguson's [1977] "signature bobs;" also equivalent to Distel and Veazy's [1982] "stereotyped head-nodding") and chases.

During each sample, I noted the time of any change in location or in behavior category; thus, the focal sample provides a continuous record of animal activity. Samples lasted from 10 to 180 minutes. I collected 56.3 h of focal data from 16 males, with samples distributed among males of all status (see below). Another 17.4 h of less intense focal samples, mostly on difficult-to-observe subordinate males, allowed the calculation of courtship and copulation rates for those males.

To map home ranges, I used two censusing techniques. First, I conducted 56 "haphazard censuses," with sample times being distributed evenly across the 2.5 month breeding season and throughout the 0730 - 1700 h activity period. During each haphazard census, I walked slowly through the study areas, locating all individuals (marked or unmarked) with the aid of binoculars and pinpointing their locations on the scale map. During these censuses I noted the behavior category (using the same categories as for the focal males, above) and any chance observations of courtship or agonistic behavior. Second, I conducted "focal censuses" of all visible C. similis every 30 minutes during focal samples. The focal censuses provide location and behavioral information on all individuals with which the focal males could potentially interact. To quantify female philopatry, I designated "female basking home ranges" as those areas in which females were observed motionless during focal censuses. I used the minimum polygon method to delineate basking areas for each female.

Determination of Male Dominance

I observed 43 male-male interactions in which I could clearly designate a winner and loser, including 35 chases, six supplants/displacements, and two fights. Based on these observations, I placed all males into one of three dominance categories: *dominant* males are those that chased all other males within their range but were never observed to be chased or intimidated by any other male; *subordinate* males were the lowest-ranking males, and never were seen to chase any other male; *mid-rank* males were chased by dominant males, but chased subordinate males. No reversal of dominance was ever indicated, and the ease of observability of dominant and mid-rank males assured the correct rank assignment of those males. Smaller males, however, are more furtive and difficult to observe, and some "subordinate" males may have engaged in chases that I did not detect. For some analyses (i.e., those in which sample sizes for subordinate males were limited), I lumped mid-rank and subordinate males into one "low rank" category.

Courtship Behavior and Female Response

I observed 91 courtship sequences, including 12 copulations (47 of the courtships and six of the copulations were from focal samples; the remainder were from haphazard censuses and other opportunistic sampling). Courtship in C. similis begins when the male initiates vibratory head-nodding and begins to circle the female or move alongside her. If the courtship continues, the male grasps the female's neck in his jaws; he may hold her for several minutes before moving his tail beneath hers, which I designate as the onset of copulation. For each courtship sequence, I timed the events and categorized the behaviors that led to the cessation of courtship as follows: a) *female leaves;* the female moves more than 3 m from the male or makes herself unavailable, e.g., running down a burrow; b) *tailslap;* the female strikes the male with her tail, usually on his snout; c) *male stops;* the male ceases head nodding even though the female has moved less than 2 m and has not used the tailslap; d) *male chase;* the male is chased by another male, or leaves to chase another male. These four categories are mutually exclusive. I did not include in the analyses any ambiguous outcomes (e.g., female moving between 2 and 3 m from the male). Once the neckgrab was attained, I classified as "female resistance" any sequence in which the female struggled. The difficulty of implying female intent in these struggles is somewhat mitigated by the fact that in all cases, the struggles were unambiguous, even bordering on the violent. Females often rolled over on their backs, and in one case a female lost her tail tip during the thrashings that accompanied resistance. As testament to the earnestness of these struggles, over half of those females that struggled did escape the neckgrab of the male and ran down a burrow immediately.

Statistical Methods

To examine allometric differences among groups in morphology, I analyzed the residuals of the regression between body length and the variable of interest. This allowed examination of morphological differences among groups that are independent of body size. In analyzing courtship outcomes, I treated each courtship as a statistically independent event as opposed to repeated measures for individual males. To test the hypothesis that the frequency of courtship outcomes varied with male status, I analyzed courtship outcomes with a contingency table analysis, which uses the null model that courtship outcome is independent of male status. T-tests are unpaired except where indicated. Data analyses were conducted with Statview IV (Abacus Concepts. 1992) and SuperANOVA (Abacus Concepts, 1989). I followed the methodology of Cohen (1988) in computing power analyses.

RESULTS

Overall Activity Patterns

Ctenosaura similis spend most of their time motionless. Movements were infrequent among males of all status; however, dominant males spent more time in sun exposure than did males of low rank (mid-rank and subordinate males combined; Table 1). Both dominant and low-rank males spent less than 10% of their time moving and feeding (Table 1). Display rates differed, however; dominant males used the assertion head-bob at a higher rate than the two combined categores of low-rank males ($t_{14} = 3.114$, $p = 0.0076$; Table 2). If low-rank males are not lumped, dominant males differed in display rate compared with subordinate males (ANOVA, $F_{2,13} = 5.174$, $p = 0.0222$; Scheffe post-hoc $p = 0.0273$) but not with mid-rank males ($p = 0.1004$; $1 - \beta \geq 0.58$; power extrapolated from Table 2.3.5, Cohen 1988).

Female Habitat Use and Home Range Distribution

Most of the forest habitat at Palo Verde was not used by adult C. similis; rather, populations occured in isolated clearings, treefall gaps, and near exposed limestone outcrops. Within these areas, which ranged in size from approx. 0.4 - 1 ha, adults were localized around specific hollow trees, rock outcrops with deep crevices, or small areas with a high density of burrows (which are dug by the females and are permanent). The distribution of females was closely tied to these retreats; of 320 female sightings during haphazard and focal censuses, 206 (64.4%) were stationary and within 2 m of a retreat (burrow, hollow tree, or rock crevice). Such retreats formed the nuclei of female activity, with very high home range overlap within these areas (Figs. 1A, 2).

Food was a secondary factor affecting female distribution and movements. Ctenosaura similis at Palo Verde fed on tree flowers, with herbaceous annuals following in importance (Table 3). Several trees at Palo Verde, particularly Bombacopsis quinatum and Tabebuia ochracea, drop large numbers of flowers over a period lasting days to weeks, resulting in localized concentrations of a highly preferred food source. Another food source that resulted in a clumped distribution of feedings were the flowers of mango trees, Mangifera indica, which the lizards climbed to feed. Observed feeding events on the only other food sources utilized, the foliage of unidentified herbaceous plants and the relatively small deciduous flowers of Masticodendron capiri, were more widely scattered. I designated as "feeding sites" all sites surrounding flowering trees in which more than 10 feedings were observed. Since these feeding sites were spatially separated from the burrow areas (defined as the areas encompassed by female basking home ranges; Fig. 1), the distribution of females was bimodal: of 320 sightings from haphazard and focal samples, most were either within the basking home range (84.4%) or at feeding sites (9.1%), with most long-range movements being between the two.

Male Dominance and Home Range

Like the distribution of females, the dominance hierarchy among males was based on the locations of burrow areas, with each of the seven observed dominant males defending such a site and all other males remaining on the periphery of the dominant male's territory or at feeding sites (Figs. 1B, 2). Thus, each burrow area contained one dominant male surrounded by two to six low-rank males. There was a significant difference in location among males of different status ($F_{2,25} = 18.9$, $p < 0.0001$). Dominant males were sighted within female basking home ranges significantly more than either mid-rank or subordinate males (Scheffe post-hoc; $p = 0.0023$ and $p < 0.0001$, respectively), although incursions into these areas by low-rank males did occur. This territorial arrangement resulted in a greater proximity to females for dominant than low-rank males. The mean distance between a male and the nearest female (taken from focal censuses) was lower for the seven dominant males than for the 15 most observable low-rank males ($t_{20} = 5.57$, $p < 0.0001$). The number of females within 5 m of a male during the censuses was also greater for the dominant males than for the 15 low-rank males ($t_{20} = 9.72$, $p < 0.0001$).

Courtship and Copulatory Behavior

Most courtship events were halted before the male grasped the female's neck in his jaws, which is a necessary prerequisite to copulation (Fig. 3). Of 90 complete courtship sequences, 26 (28.9%) ended before the neckgrab when the female left the area or struck the male with her tail. However, males often ceased courtship on their own, even when the female had moved less than 2 m and had shown no signs of apparent resistance or rejection (N = 30; 33.3%). Male chases caused the termination of an additional 10 (12.2%) courtships before the neckgrab. Copulation was still not assured even after the neckgrab had been attained; of 24 neckgrabs, only 14 resulted in a confirmed copulation, with the remainder ending due to the female's struggles (N = 5) or to the male being chased by a male of higher status (N = 3) (an additional two females were dragged out of sight by males, and the outcomes are unknown). Some females continued to struggle during the copulation (N = 2), although in most copulations there was no excessive movement by the female.

Males of different status differed in the location in which they courted. Forty-five of 56 courtships (80.4%) by dominant males (N = 6 males) took place within female basking home ranges. Among 43 courtships by 14 low-rank males, however, 24 (55.8%) were in the basking home ranges, 8 (18.6%) took place in feeding areas, and 11 (25.6%) took place between the basking home ranges and the feeding areas. Most of the courtships by low-rank males within the female basking areas consisted of attempted "sneak" copulations, and differed from the courtships of dominant males (see below).

Although dominant and low-rank males utilized the same suite of movements to court females, courtships by subordinate and mid-rank males tended to be quicker than those of dominant males. The normal range of times spent in the pre-neckgrab portion of courtship were 0 - 513 sec for low-rank males, and 5 - 686 sec for dominant males (this does not include one 1001 sec courtship by a mid-rank male that was excluded from these analyses because it was more than 4 standard deviations from the mean). Dominant males spent more time in the pre-neckgrab portion of courtship than did low-rank males (t-test, $t_{77} = 3.165$, $p = 0.0022$). Including the 1001-sec outlier renders this relationship marginally significant ($t_{78} = 1.948$, $p = 0.055$; $1 - \beta \geq 0.99$). The courtships of dominant males included more bouts of vibratory head-nodding than did those of low-rank males (4.9 and 2.0, respectively; $t_{35} = 2.271$, $p = 0.0294$). There was no difference between dominant and low-rank males in the total portion of the time budget spent courting (t_{13} = 0.906, p = 0.3815; Table 2).

The stage at which courtship ended and the causes of courtship termination varied with male status, and both male behavior and female response contributed to these differences. Dominant males were more likely to stop courting before the neckgrab than either mid-rank or subordinate males (Table 4, Fig. 4). Chases by other males were a significant factor in the courtship outcomes for mid-rank males, but not dominant males. Females also responded differently to males of different status by leaving dominant males less frequently than either mid-rank or subordinate males; however, there was no difference in the frequency of the tailslap for males of different status (Table 4). Once the neckgrab was attained, females were less likely to resist dominant males (Table 4, Fig. 4). Many of the neckgrabs of low-rank males were terminated before copulation, either by female escape (N = 5) or chases/intimidation by other males (N = 3). In four cases in which low-rank males courted females in the territory of the dominant male, they did so rapidly and grasped the female's neck and attempted to drag her away from the dominant male's territory. All four were resisted vigorously, and two of the females escaped (these two are included in the category "female escapes neckgrab" on Fig. 3). The other two were dragged out of sight by the low-rank males, and the outcomes of those "courtships" were unknown. The termination of courtships of low-rank males due to female resistance and intimidation by dominant males was largely responsible for the higher overall copulation rate of dominant males (21.4%, 6.1%, and 0%, respectively, for dominant, mid-rank, and subordinate males). Mid-rank males were significantly more likely to be resisted during copulation than dominant males (Table 4).

Sexual Dimorphism and Fighting Behavior

Ctenosaura similis is highly dimorphic both in size and head dimensions. Males had longer bodies and weighed more than females ($t_{56} = -5.975$, $p < 0.0001$ and $t_{56} = -7.009$, $p < 0.0001$, respectively), and had proportionately longer, higher, and wider heads (t-tests on the residuals of the log body length (BL) - log head length (HL) common regression for both sexes; $t_{56} = -6.556$, $p < 0.0001$; $t_{56} = -4.619$, $p < 0.0001$; and $t_{56} = -5.523$, $p < 0.0001$, respectively; Fig. 5).

Dominant males did not significantly differ from mid-rank males in body length or mass (ANOVA; $F_{2,18} = 15.595$, $p = 0.0001$, Scheffe post hoc $p = 0.9551$; and $F_{2,18} = 18.233$, $p < 0.0001$, Scheffe post hoc $p = 0.9795$, respectively), but both dominant and mid-rank males have longer bodies and greater mass than subordinate males (Scheffe post hoc; dominant-subordinate comparisons: $p = 0.006$ and $p = 0.0002$; mid-rank-subordinate comparisons: $p = 0.0016$ and $p = 0.0009$). Dominant males also differed from low-rank males (mid-rank and subordinate status lumped) in having proportionately longer heads (Fig. 6). However, dominant males did not differ from low-rank males in proportional head height, head width, or body mass (t-tests on residuals of the regressions of these variables on log BL; $t_{19} = 1.5$, $p = 0.15$; $t_{19} = 0.665$, $p = 0.5139$; and $t_{19} = 0.747$, $p = 0.4641$, respectively).

I witnessed the use of the head during male-male contests in three separate instances, the only times I observed physical contact between adult males. Each encounter followed a prolonged series of lateral displays and assertion head-nodding between two more or less size-matched males. The two then faced in opposition to one another and each laid its head against the flank of its opponent with the mouth gaping to its maximum extent. They would alternate remaining motionless in this gaping posture, jaws in contact with but not biting down on their opponent, with bouts of lunging and pushing against one another (Fig. 7). At no time was actual biting observed.

DISCUSSION

The evolution of polygynous mating systems is often linked to moderate levels of synchrony in breeding, coupled with the uneven distribution of critical resources (Emlen and Oring 1977). In C. similis, several factors may contribute to the intense levels of local mate competition and the resultant patterns of social behavior and sexual dimorphism.

Spatial Distribution and Resource Use

The distribution of C. similis at Palo Verde is clumped at two different scales. On a landscape scale, most forested land in the park is not frequented by the lizards; rather, they are locally common in clearings and other semiopen habitats in which sunlight reaches the ground. At a local scale, within the semiopen areas, females are highly clumped in distribution, with burrow entrances forming the nucleus of each "hotspot" of female activity. Four of the seven hotspots studied were centered on large hollow trees with numerous openings; two of them included patches of burrows dug into sandy soil, and one was centered on a limestone outcrop with deep crevices.

The landscape-scale pattern of reliance on relatively open macrohabitats may be due to thermal benefits of these areas over adjacent closed-canopy forest, since thermal factors are important in the habitat choice of other large-bodied iguanids (Christian et al. 1983; Christian and Tracy 1985; Rauch 1985; van Marken Lichtenbelt et al. 1993). The higher proportion of time spent basking in the sun by dominant males relative to low-rank males is consistent with the notion of a thermal benefit to high-quality territories. However, the burrows around which females clumped at the smaller scale were clearly not determined solely by sun exposure; some of the burrow areas were exposed to sun while others were relatively shaded. At the local scale, the burrows themselves were the only invariant feature. Iguanids as a group show a heavy reliance on the presence of refuges, either natural retreats (e.g., rock crevices) or friable soil for burrowing (Evans 1951, Berry 1974, Iverson 1979, Carothers 1981, Case 1982, Dugan and Wiewandt 1982). These retreats are permanent, and often used by the same individual lizard in consecutive years, as has been shown for C. similis at Palo Verde (Burger and Gochfeld 1991). In part, this reliance on permanent refuges by members of the family Iguanidae may be due to their large body size, which is thought to have evolved in response to the demands of an herbivorous diet (Pough 1973, Van Devender 1982, Zimmerman and Tracy 1989). In contrast to insectivorous lizards, most of which weigh less than 50 g, home ranges of large-bodied iguanids such as C. similis (adult females at Palo Verde average 991.9 g; males average 1836.7 g) will likely have fewer retreats suitable for escape from predation. This disadvantage of large body size, however, may be partly offset by a smaller potential predator pool as well as increased running ability: although burst speed is mass-independent in C. similis, endurance scales positively with mass (Garland 1984).

In addition to the burrows, the distribution of the preferred food source led to a secondary clumping of females in time and space, and offered low-rank males a strategy for obtaining copulations. Plant food is often less evenly distributed than insects, and this has been implicated in the development of polygyny in other iguanids (Krekorian 1976, Carothers 1981). The clumped nature of feedings in C. similis is further exaggerated because breeding coincides with the deciduous season in Palo Verde, and the tree flowers provide localized pulses of highly preferred food in an otherwise foliage-depauperate environment. An advantage gained by this particular breeding phenology is that the eggs, which are laid in March (Fitch and Hackforth-Jones 1983, Mora 1989), will hatch at the onset of the rainy season in May, a time of extremely high productivity conducive to rapid growth of the hatchlings (Van Devender 1982).

Male Dominance

Male C. similis exhibit a clear dominance hierarchy that is stable over the course of the breeding season. Although territorial incursions by low-rank males and resultant displays and chases by dominant males are common, fights are rare and no dominance reversals were observed. Dominant and mid-rank males exhibited a high degree of site fidelity, with the female basking home ranges clearly at the center of the dominant males' defended areas (Figs. 1B, 2). Mid-rank males arranged themselves on the periphery of the dominant males' territories and/or the nearby feeding areas, where such areas occurred. Subordinate males were more rarely seen, and this could be attributed to a relative lack of territorial behavior by these males, as evidenced by the low display rates of subordinates relative to both dominant and mid-rank males. It is likely that subordinate males are the youngest reproductive males, as their smaller body size suggests (Table 1).

The two-step dominance hierarchy observed in this population is reminiscent of other iguanids, such as Sauromalus obesus (Berry 1974), Ctenosaura hemilopha (Carothers 1981), and C. pectinata (Evans 1951), that rely on isolated rockpiles for predator refuges, but similar dominance hierarchies are rare in lizards in general. One-step hierarchies are the rule in polygynous insectivorous species, perhaps partly a result of a more widely dispersed food and refuge distribution as well as (usually) larger population sizes which enhance the ability of low-status males to find mates (Stamps 1983). The absence of territorial behavior in subordinate male C. similis indicates that suitable habitat is limiting at Palo Verde, and males may simply forego territoriality until they reach a body size that allows them to defend either the feeding sites (as mid-ranks) or the female basking sites (as dominants).

Courtship and Copulatory Behavior

As with any polygynous system by definition, copulation success among male C. similis is skewed, with dominant males obtaining most copulations and subordinate males achieving the fewest. This disparity is due not only to male-male interactions, which set the stage by limiting access of low-rank males to females, but also to the responses of females to males during the courtship process, since courtship termination by female behavior was commonly observed.

Dominant male C. similis courted females almost exclusively in the basking home ranges; the relatively large proportion of courtships by low-rank males in and near the feeding areas indicates that those males were intercepting females and courting them during their foraging movements. Thus, low-rank males were attempting to court moving targets, since females at the feeding sites rarely remained for long. In contrast, dominant males courted females where they were sedentary and predictably located. Courtships by dominant males also differ in being less intense; dominant male courtships (prior to the neckgrab) are of longer duration and include more bouts of vibratory head-nodding. Dominant males are also more likely to stop courting in the absence of female resistance than low-rank males. The relatively quick, intense courtships of low-rank males may arise from the necessity of courting a female that is only briefly available in the feeding area. Alternatively, courtship time is limited for a low-rank male attempting a sneak copulation inside the territory of the dominant male. Indeed, in several instances mid-rank males siezed females in the territory of the dominant male and dragged or attempted to drag them out of the area before being detected by the dominant male. In general, chases by higher-ranking males were an important cause of courtship terminations in low-rank males, both before and during the neckgrab.

Females respond differently to the courtship advances of males of different status. They are less likely to leave a dominant male than a low-rank male during the pre-neckgrab phase of courtship, and they are more likely to resist the neckgrab of a low-rank male. They use the tailslap with equal frequency against dominant and low-rank males, however. These rejection behaviors may be a response to the nature of the courtship, since low-rank males are more likely to attempt a neckgrab early in the courtship. Alternatively, females may be responding to male identity *per se*, resisting poor-quality males independently of the style of their courtship. Female choice of male morphological traits has rarely been demonstrated in lizards (Olsson and Madsen 1995), and in *C. similis* there is clearly a need to tease apart the variables of male identity/morphology and courtship style before such a conclusion could be made. Female *C. similis* behavior still may be considered a form of mate choice, however, since it clearly contributes to the variance in mating success between males of different status (Tokarz 1995). Low receptivity toward males regardless of status is considered a form of mate choice (Cox and LeBouef 1977) in that it ensures that the only males that will achieve copulations are those able to invest the necessary time in courtship or fend off other males. Female rejection of male courtship is common in lizards (Stamps 1983), but in few species do males force copulations with unwilling females (e.g., *Tropidurus delanonis* [Werner 1978], *Uta palmeri* [Hews 1990], *Iguana iguana* [Rodda 1992], and *Ctenophorus maculosus* [Olsson 1995]). Such behaviors may evolve in males when a) receptive females are limiting in numbers or unavailable to certain males, b) females are small relative to males, and therefore unable to completely resist the males' attempts, and c) mechanisms of fertilization, such as sperm storage (Cuellar 1966), allow for a gain in reproductive success of the male that forces a copulation. Although the mechanism of fertilization is unknown in *C. similis*, the first two of these predictions certainly hold true. and the extremely high clutch size of this species (mean clutch size for Nicaraguan populations = 43; Fitch and Henderson 1978) indicates a realistic possibility of multiple paternity within a clutch.

Sexual Dimorphism and Fighting Behavior

Ctenosaura similis exhibits a high degree of sexual dimorphism both in body size and in the allometry of the head. Sexual dimorphism in body size is common among polygynous lizards (Stamps 1983), and is expected to be most obvious in large-bodied. long-lived species such as C. similis. An unexpected result of my study, however, is the dimorphism in head length among males of different status: dominant males have longer heads, independent of body size.

Carothers (1984) found a positive association between male aggressiveness and head dimorphism in iguanids, and attributed the evolution of sexual dimorphism within this family to intrasexual selection. Specifically, he hypothesized that increased gape and bite strength increased the ability of males to defend favored territories and obtain access to females. In phrynosomatids (Hews 1990) and scincids (Vitt and Cooper 1985), males with larger head dimensions have an advantage in combat. The advantage may extend to the actual mechanics of copulation as well, since the added bite strength could improve the ability of males--particularly small males struggling with unreceptive females--to maintain a grip on the females prior to and during intromission.

It is unknown whether a longer head in C. similis improves the bite strength, which would seem to be more strongly correlated with head width or depth (e.g., Vitt and Cooper 1985, Hews 1990). However, male C. similis with longer heads may have an advantage in male-male combat. These fights involved the animals gaping and laying their jaws along the flank of their opponent (Fig. 7), but at no time did I detect actual biting. Rather, the contest seemed to serve as an assessment match; the advantage of a proportionally longer head could be in presenting an opponent with a larger gape during these contests. A much larger sample size, with head-length analyses of winners vs. losers, would be needed to test this hypothesis. It is likely that more fights take place in the weeks and/or months leading up to the breeding season, and investigating the dynamics of male combat and territory establishment at this time could prove productive. Although fights are rare, they may be evolutionarily important events, since the outcomes may determine the seasonal reproductive success of the males involved.

CONCLUSIONS

My results indicate complex interactions among resource distribution, mating strategies, and resultant patterns of mating success and sexual dimorphism in Ctenosaura similis. Much of the social biology of this species seems tied to the reliance of females on resources that are clumped at different scales. Female clumping around burrows and other refuges allows the monopolization of females by a small number of behaviorally dominant males, but reliance on a spatially patchy food supply that does not coincide spatially with refuges ensures that this monopolization is incomplete, and sets the stage for the evolution of alternative mating tactics in low-rank males. Males vary in mating success, with dominant males achieving most copulations. Both male-male interactions and female responses to male courtship contribute to this variance in mating success. Sexual dimorphism in C. similis may be related to the nature of intrasexual selection.

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Table 1. Activity of male C. similis as a function of status; mid-rank and subordinate males lumped as "low rank" (means ± st. dev.; t-tests, * = $p < 0.05$). Data are mean percentages of time spent in a given category, from 56.3 h of focal observations. The categories "stationary under cloud cover" (overall mean = 6.33% ± 19.9) and "interacting" (overall mean = 1.28% ± 3.04) are not included in this table.

Activity Category	Dominant Males	Low Rank Males	Overall Means
Stationary in sun	63.08 ± 19.16	32.97 ± 27.49	*
Stationary in shade	23.93 ± 13.35	44.57 ± 32.42	38.12 ± 29.08
Feeding	1.56 ± 2.67	6.9 ± 12.79	5.23 ± 10.84
Moving	2.68 ± 2.18	3.69 ± 7.64	3.42 ± 6.55
Moves per minute	0.19 ± 0.31	0.08 ± 0.08	0.11 ± 0.18

Table 2. Dominance designations, size (body length / head length, in mm) and behaviors (means ± st. dev.) of male C. similis, from a total of 73.7 h of focal observations. d = dominant; m = mid-rank; s = subordinate (see text for explanation of dominance assignment). Uncaptured males (not assigned i.d. numbers) were identified by idiosyncrasies of size, shape, and color, and morphological data on these animals are not available. % time courting indicates the proportion of time spent in courtship during focal sampling; # females courted includes all marked females seen courted by this male, including those observed during haphazard censuses and focal sampling; "+" indicate courtships with females of unknown identity.

Male	Status	BL / HL	Headbobs/ min	% time courting	# females courted
9	d	287.1 / 102.9	0.42 ± 0	0 ± 0	0
25	d	278.0 / 107.0	0.45 ± 0.21	0 ± 0	1
115	d	266.4 / 103.6	0.35 ± 0.17	3.4 ± 6.4	7+
48	d	290.4 / 114.6	0.32 ± 0.26	7.5 ± 12.5	6+
42	d	278.7 / 106.3	0.52 ± 0.212	0.3 ± 0.4	1
Means:		**280.1 / 106.9**	**0.41 ± 0.08**	**2.2 ± 3.3**	**3**
5	m	276.5 / 108.5	0.44 ± 0.11	3.2 ± 4.6	1
10	m	294.5 / 105.5	0.3 ± 0	1.1 ± 0	1
38	m	275.1 / 94.9	0.08 ± 0.12	5.2 ± 13.4	13+

Table 2 continued.

Male	Status	BL / HL	Headbobs/ min	% time courting	# females courted
55	m	290.8 / 104.2	0.08 ± 0.09	0 ± 0	0
DEF	m		0.02 ± 0.05	0 ± 0	1
DB2	m		0.36 ± 0.02	0.2 ± 0.3	1
Means:		**284.2 / 103.3**	**0.21 ± 0.18**	**1.6 ± 2.1**	**2.8**
31	s	206.0 / 64.0	0 ± 0	1 ± 0	2
33	s	266.0 / 94.0	0.24 ± 0	0 ± 0	0
40	s	218.6 / 76.4	0.15 ± 0		1
NEW	s		0.3 ± 0	0 ± 0	0
CEI	s		0 ± 0	0 ± 0	0
Means:		**230.2 / 78.13**	**0.14 ± 0.14**	**0.25 ± 0.5**	**0.6**

Table 3. Observed feeding events by Ctenosaura similis at Palo Verde.

Plant	Family	flowers/ foliage	# observed feedings	% total feedings
Bombacopsis quinatum	Bombacaceae	flowers	16	21.6
Masticodendron capiri	Sapotaceae	flowers	3	4.1
Tabebuia ochracea	Bignoniaceae	flowers	11	14.9
Mangifera indica	Anacardiaceae	flowers	22	29.7
Unidentified annuals		foliage	22	29.7

Table 4. Post-hoc contributions to differences in courtship behaviors among male C. similis of different status. Contributions with absolute values of > 1.96 are significantly different from the null model (Chi Square = 44.225; p = 0.0002; contingency coefficient = 0.574), and are indicated in boldface.

	dominant	mid-rank	subordinate
female leaves	**-2.256**	1.278	1.690
tailslap	0.733	-0.232	-0.845
male stops	**3.283**	**-1.999**	**-2.236**
male chased	**-3.098**	**2.275**	1.482
male chases another male	1.368	-1.114	-0.477
neckgrab resisted	**-2.880**	1.912	1.706
male chased, post-neckgrab	-1.842	1.050	1.370
copulation, female resists	-0.064	0.361	-0.477
copulation, no resistance	**2.938**	**-2.260**	-1.240

FIGURE LEGENDS

Figure 1. (A) Female home ranges (closed polygons) associated with one of the clumps of burrows (burrow openings indicated by stars), and nearby feeding areas (dashed ellipses). Each female home range is based on sightings of basking individuals ($\bar{x}$ no. of sightings per female = 10.6); sample sightings for two females (□, ◇) are included to illustrate the clumped nature of sightings within a home range. The feeding areas indicated include two Mangifera trees within the smaller ellipse and a Tabebuia tree within the larger one. (B) Sightings of dominant, mid-rank, and subordinate males at the same locality, superimposed on the combined female basking home ranges (closed polygon) and feeding areas (dashed ellipses). Data are from haphazard and focal censuses. The remainder of the area contained no other feeding areas or burrows.

Figure 2. Burrow sites, female basking home ranges (polygons), and sightings of dominant, mid-rank, and subordinate males at two localities in the study area. (A) Four burrow sites near the OTS biological station (station building represented by rectangle). (B) Two additional sites at "the Hacienda," 1 km from the station. Dashed ellipses represent feeding areas (each contains one flowering Bombacopsis tree); no such area was identified for the Hacienda population.

Figure 3. The sequence of courtship and frequencies of events that end courtship for C. similis. Width of lines are proportional to the number of observations. See text for descriptions of behaviors.

Figure 4. (A) The frequency of courtship outcomes prior to the neckgrab, for dominant

(black bars; N = 47 events), mid-rank (shaded; N = 34), and subordinate (open; N = 9) males. (B) Frequency of outcomes given that the neckgrab has been attained (N = 24 events). See text for definitions of behavioral categories and Table 4 for statistical comparisons.

Figure 5. Regression of log body length versus log head height (A), log head width (B), and log head length (C) for adult male and female Ctenosaura similis. All regressions are significant ($p < 0.0001$).

Figure 6. Residuals of the log body length - log head length regression for adult male Ctenosaura similis, plotted against log body length to examine differences in relative head length for dominant vs. low-rank males ($t_{19} = 2.12$, $p = 0.0467$).

Figure 7. Sequence of behaviors in male-male "combat" in Ctenosaura similis. Two males approach one another (A) and align their heads alongside their opponent's flank, mouth gaping (B); they may remain in contact for a minute or more before lunging and circling one another (C).

Fig. 1

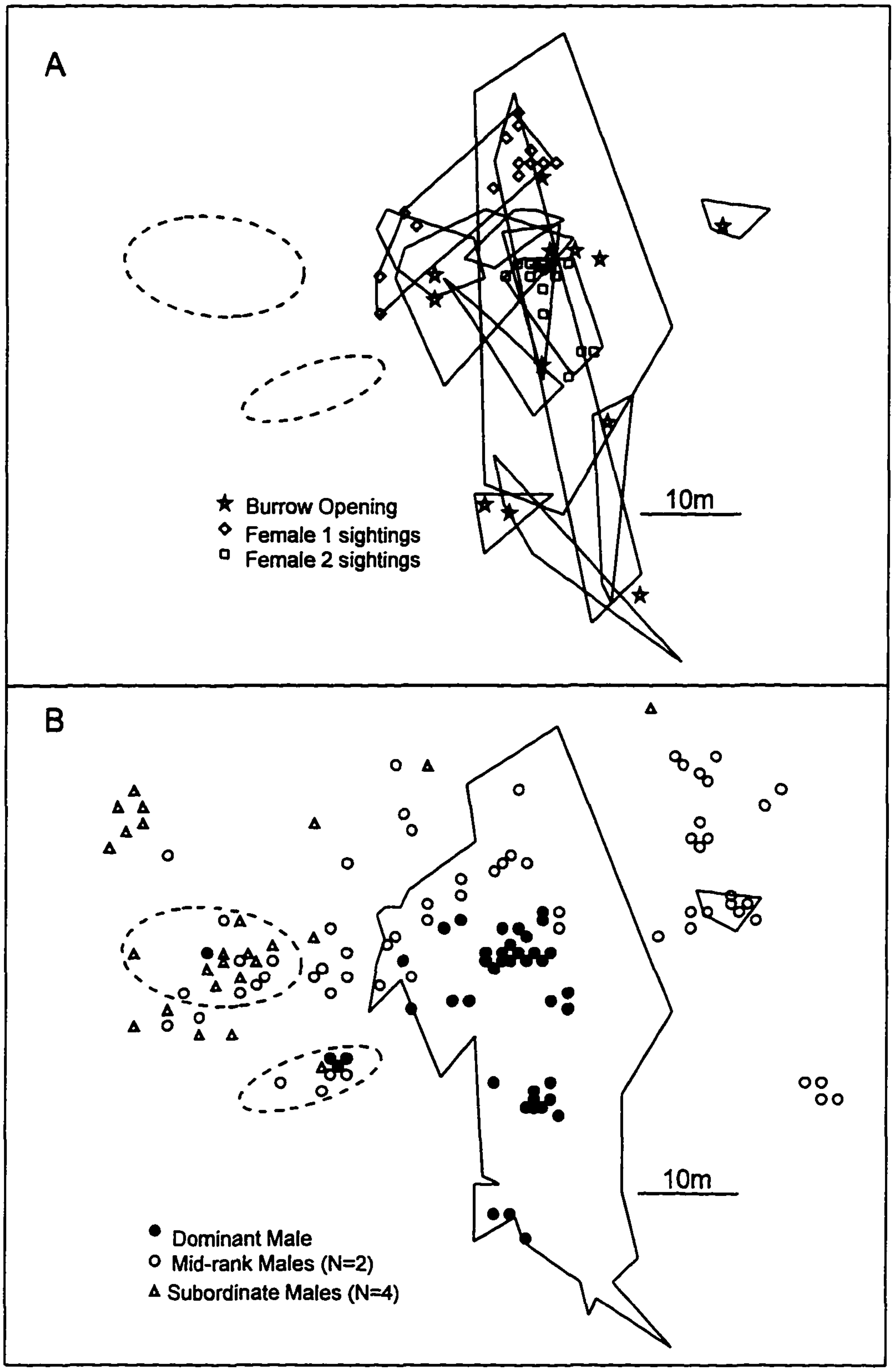

A
★ Burrow Opening
◇ Female 1 sightings
□ Female 2 sightings
10m
B
● Dominant Male
○ Mid-rank Males (N=2)
▲ Subordinate Males (N=4)
10m

Fig. 2

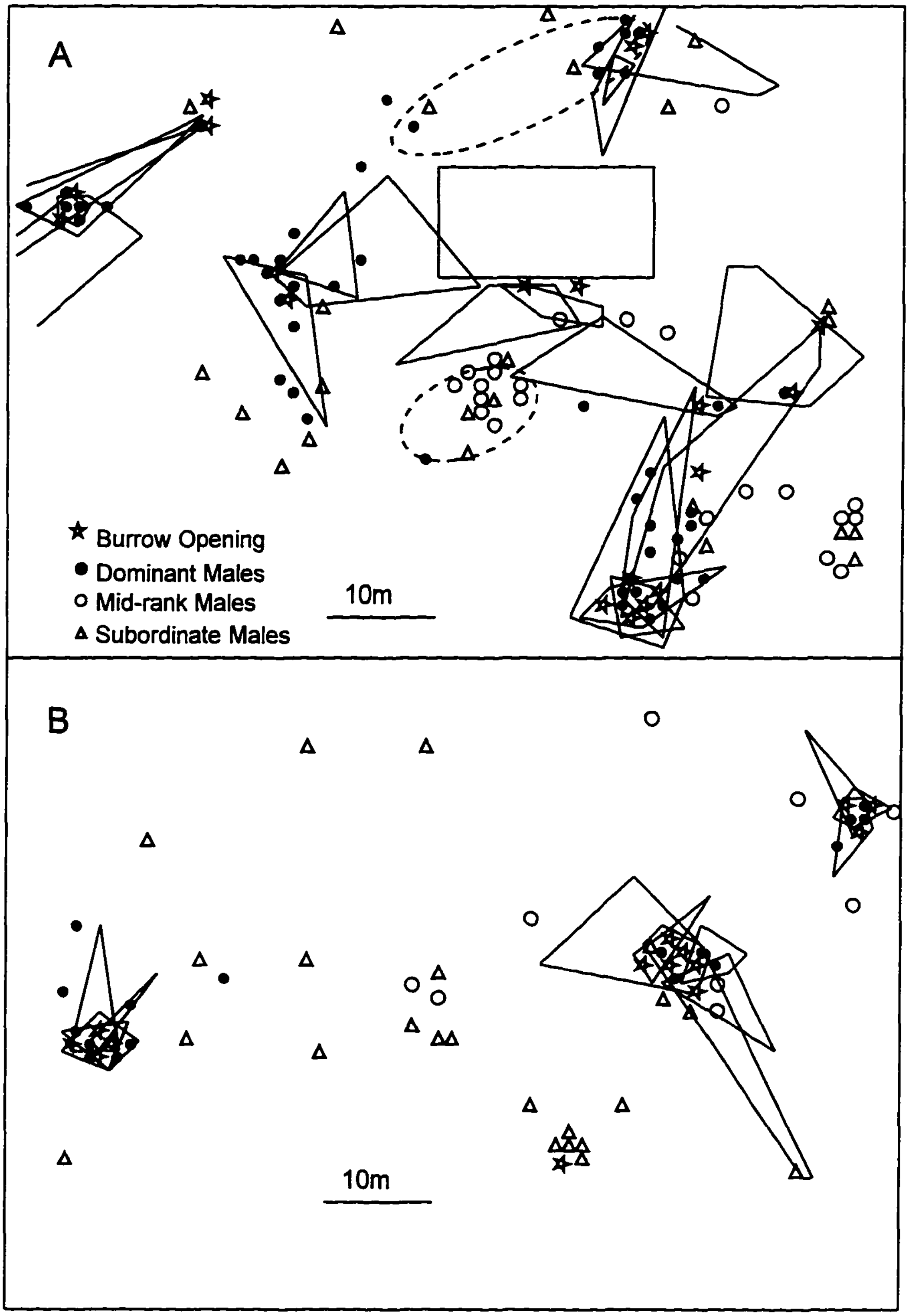

A
★ Burrow Opening
● Dominant Males
○ Mid-rank Males
△ Subordinate Males
10m
B
10m

Fig. 3

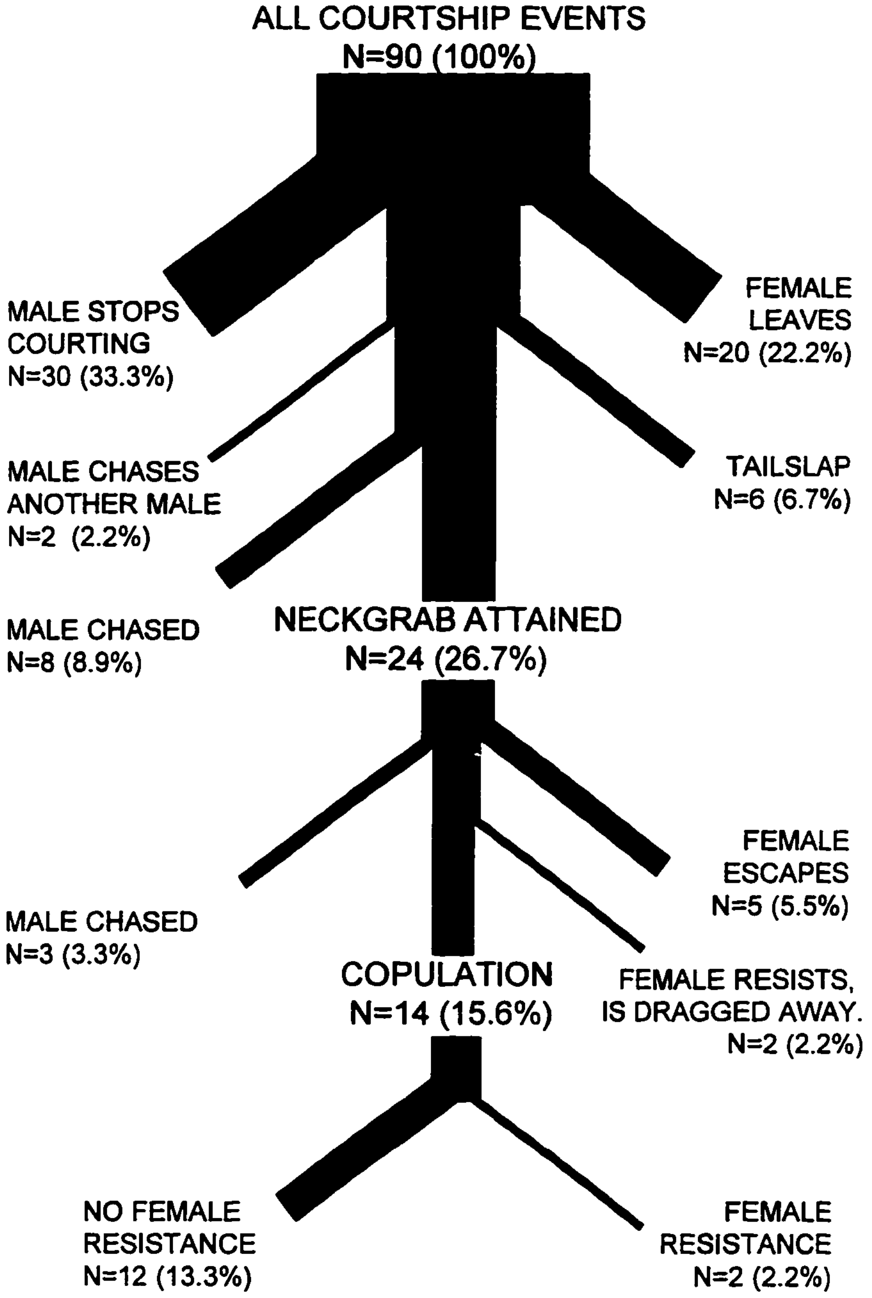
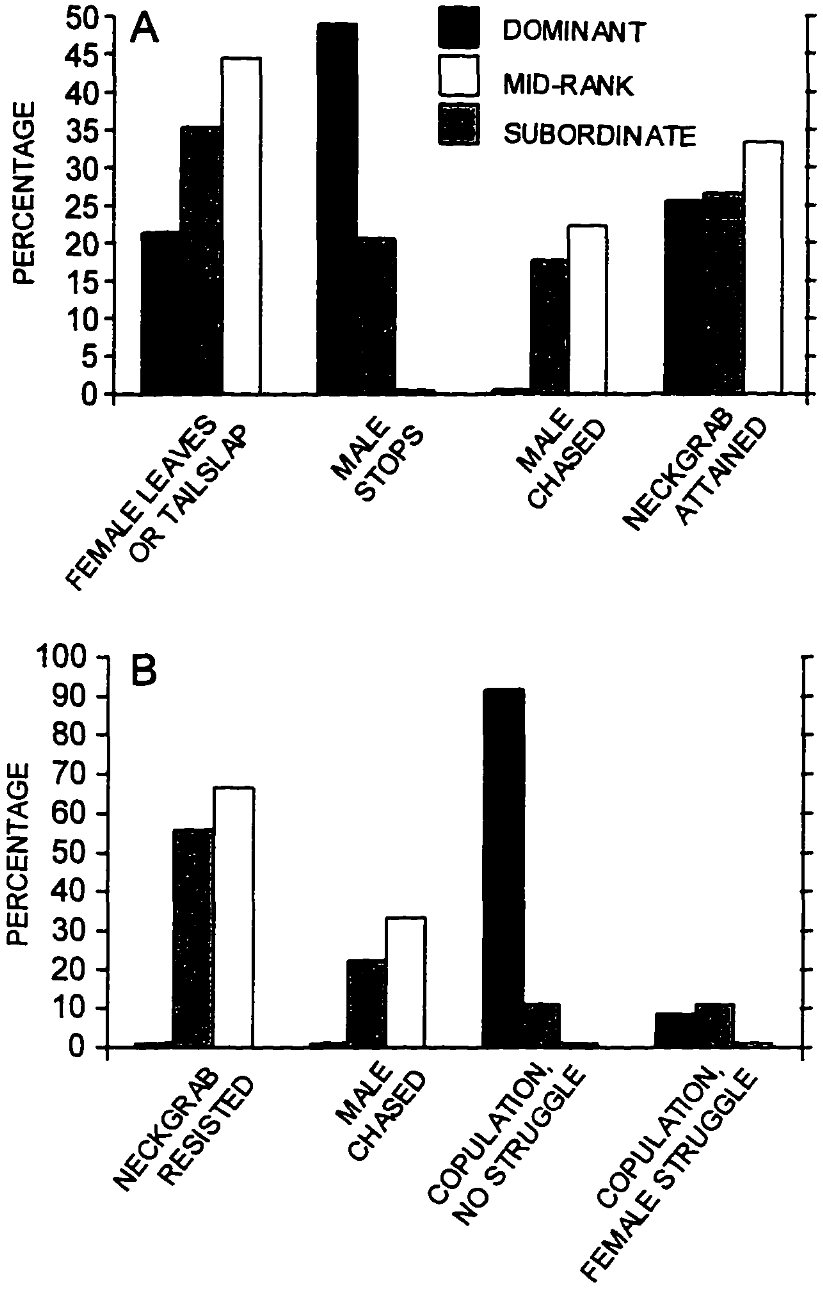

ALL COURTSHIP EVENTS
N=90 (100%)
MALE STOPS COURTING
N=30 (33.3%)
FEMALE LEAVES
N=20 (22.2%)
MALE CHASES ANOTHER MALE
N=2 (2.2%)
TAILSLAP
N=6 (6.7%)
MALE CHASED
N=8 (8.9%)
NECKGRAB ATTAINED
N=24 (26.7%)
FEMALE ESCAPES
N=5 (5.5%)
MALE CHASED
N=3 (3.3%)
COPULATION
N=14 (15.6%)
FEMALE RESISTS, IS DRAGGED AWAY.
N=2 (2.2%)
NO FEMALE RESISTANCE
N=12 (13.3%)
FEMALE RESISTANCE
N=2 (2.2%)

Fig. 4


A
PERCENTAGE
0
5
10
15
20
25
30
35
40
45
50
DOMINANT
MID-RANK
SUBORDINATE
FEMALE LEAVES OR TAILSLAP
MALE STOPS
MALE CHASED
NECKGRAB ATTAINED
B
PERCENTAGE
0
10
20
30
40
50
60
70
80
90
100
NECKGRAB RESISTED
MALE CHASED
COPULATION, NO STRUGGLE
COPULATION, FEMALE STRUGGLE

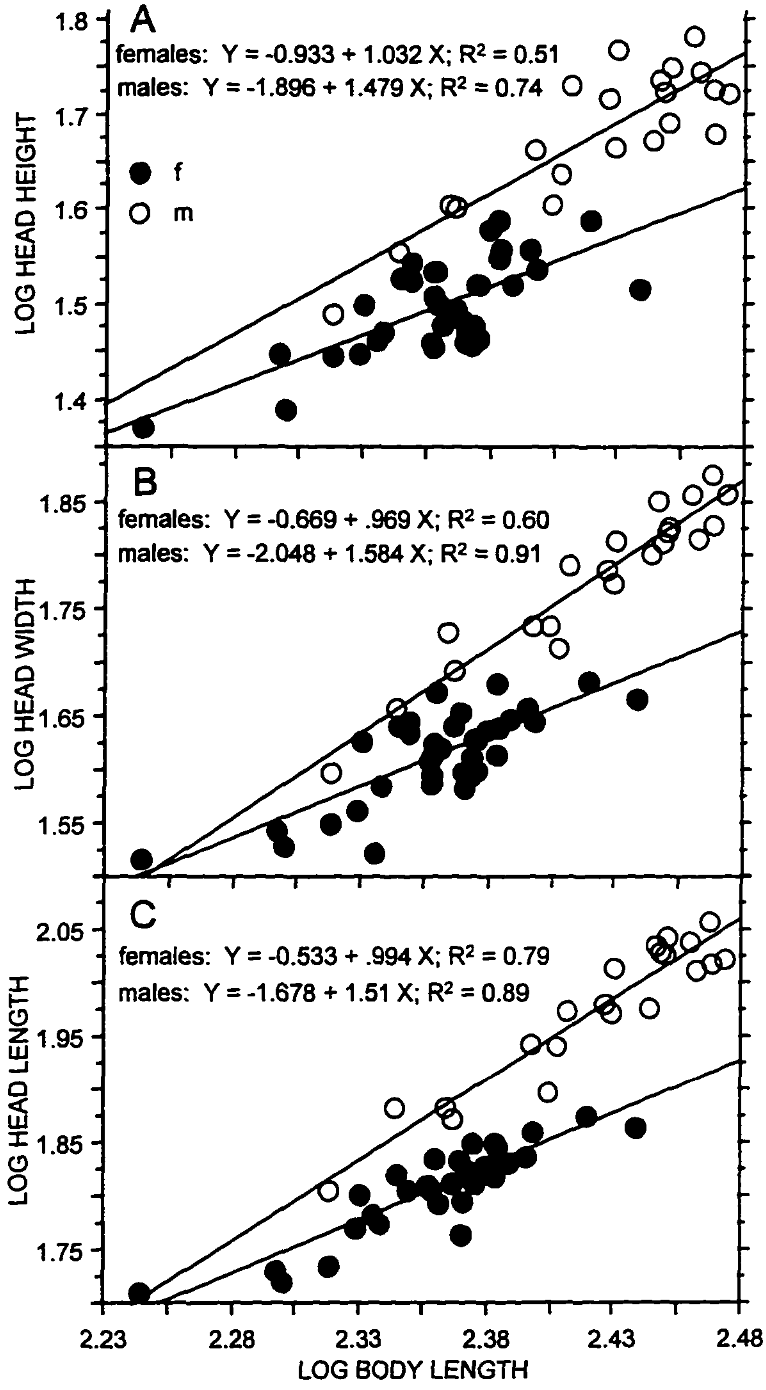
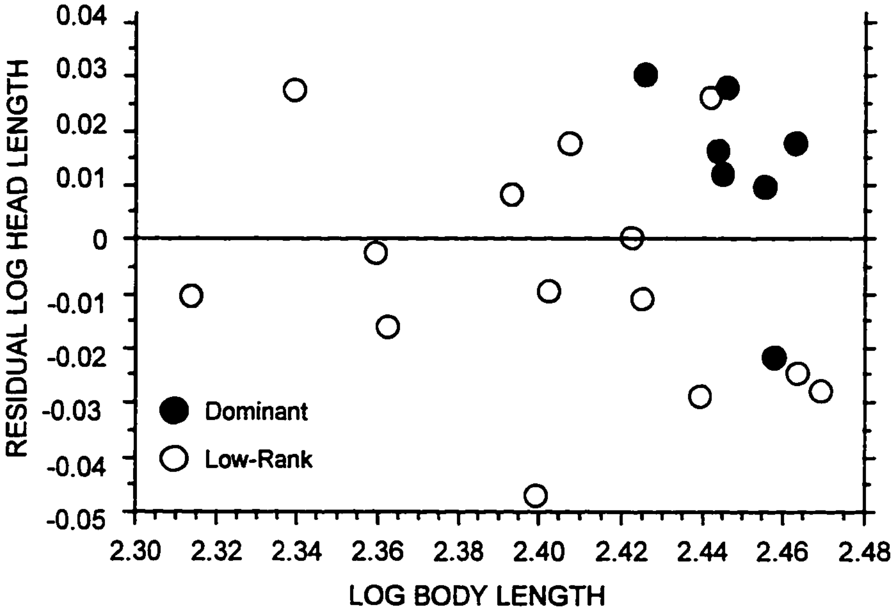
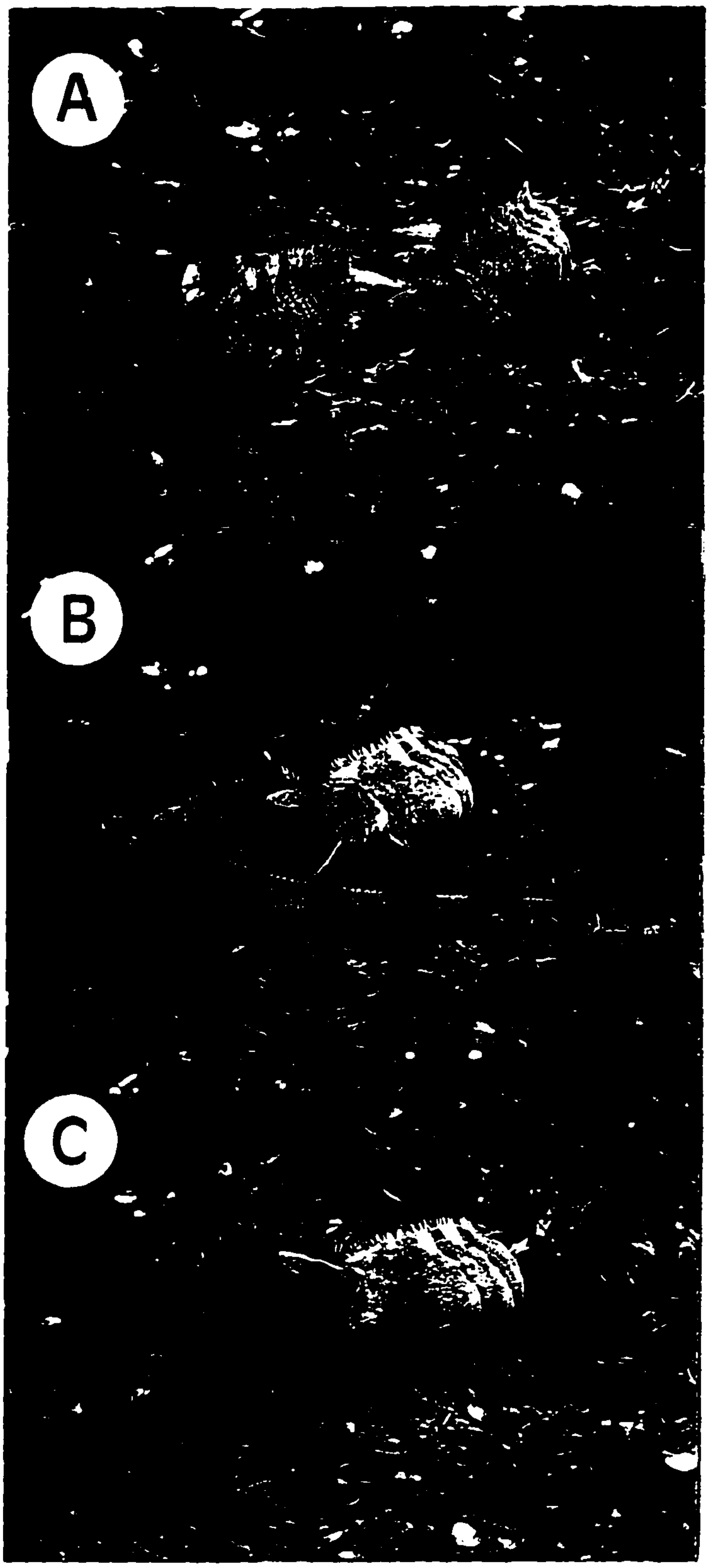

A
females: Y = -0.933 + 1.032 X; R² = 0.51
males: Y = -1.896 + 1.479 X; R² = 0.74
f
m
LOG HEAD HEIGHT
1.8
1.7
1.6
1.5
1.4
B
females: Y = -0.669 + .969 X; R² = 0.60
males: Y = -2.048 + 1.584 X; R² = 0.91
LOG HEAD WIDTH
1.85
1.75
1.65
1.55
C
females: Y = -0.533 + .994 X; R² = 0.79
males: Y = -1.678 + 1.51 X; R² = 0.89
LOG HEAD LENGTH
2.05
1.95
1.85
1.75
2.23
2.28
2.33
2.38
2.43
2.48
LOG BODY LENGTH

Fig. 5

Fig. 6


RESIDUAL LOG HEAD LENGTH
0.04
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
-0.04
-0.05
2.30
2.32
2.34
2.36
2.38
2.40
2.42
2.44
2.46
2.48
LOG BODY LENGTH
● Dominant
○ Low-Rank


A
B
C

CHAPTER 2: SOCIAL SYSTEM EVOLUTION IN A THERMALLY HOSTILE ENVIRONMENT: "COOL SPOTS" AND THE MATING SYSTEM OF *DIPSOSAURUS DORSALIS*

ABSTRACT

I investigated the mating system of the desert iguana (*Dipsosaurus dorsalis*) with the goal of understanding the ecological factors impinging on resource use and mate monopolization. I also quantified sexual dimorphism as a measure of past sexual selection. For a population of lizards inhabiting an extremely xeric dune-shrub community I examined the following: *a)* the distribution of food sources and cool-temperature microclimates; *b)* the spatial distribution of individuals relative to the measured resources; *c)* the degree of polygyny acheived by individual males as a function of the resources under their control; and *d)* the degree of sexual dimorphism and the morphological correlates of dominance among males. *Dipsosaurus dorsalis* is exposed to lethal temperatures in open microhabitats at midday; in contrast, the shrubs *Larrea tridentata* and *Chilopsis linearis* offered the coolest temperatures, and female home range overlap was highest beneath these shrubs. Although shrubs also differed in their food quality (as measured by selectivity indices), there was no correlation between female space use and the distribution of preferred food sources. Most males defended territories that included at least one female, with the most successful males (as measured by number of females courted) defending plants with the coolest shade temperatures, not those with the highest food quality. Behaviorally dominant males are significantly longer-bodied and larger-headed than low-rank males, but there were no proportional differences in

head dimensions when the effects of body length were removed. Thus, dominance in *D. dorsalis* appears to be size-based and is probably correlated with age. The absence of differences in head allometry among male status groups may explain the low degree of sexual dimorphism of *D. dorsalis* compared with other iguanids, many of which are extremely dimorphic and which at least occasionally exhibit proportional differences in head size among male classes.

INTRODUCTION

Animal body temperature represents an easily quantifiable and ecologically relevant variable, and as a result has been well studied. Links between body temperature and growth rate, microhabitat selection, and various aspects of behavior and performance are strongly supported, especially in ectotherms (e.g., Spotila, Soule, & Gates 1972; Porter *et al.* 1973; Bennett 1980; Crawford, Spotila, & Standora 1983; Waldschmidt & Tracy 1983; Dunham, Grant, & Overall 1989; Adolph 1990). One emergent property of the thermal ecology of many ectotherms is a pattern of movement and local distribution dependent on the temperature profile or "thermal map" of the habitat, as animals adjust their movement patterns relative to thermally favorable patches within their home range (Roughgarden, Porter, & Heckel 1981; Crawford *et al.* 1983; Christian & Tracy 1985; Tracy & Christian 1986; Adolph 1990; Huey 1991). A less obvious, but expected, link is the influence these movement patterns will exert on the animal's mating system and pattern of individual reproductive success. The reliance on any resource that is patchily distributed strongly influences the environmental potential for polygamy (EPP; Emlen & Oring 1977), as demonstrated for the distribution of food (Simon 1975; Bradbury &

Vehrencamp 1977; Davies & Lundberg 1984; Hews 1993), oviposition sites (Alcock 1987), and resting sites or refuges from predation (Baldi *et al.* 1996). In thermally stressful habitats, the thermal map should be a major factor determining the EPP, since thermally favorable sites will serve as defendable resources and contribute to the degree of polygamy of territory owners. However, while animal territories are influenced by thermal properties (Waldschmidt & Tracy 1983), few studies have linked the thermal properties of territories with mating success. For territories used exclusively for nesting, in lark buntings (Pleszczynska 1978) or for mating, in fur seals (Carey 1991), refuges from temperature extremes increased the degree of polygamy of territory owners. Similarly, Rauch's (1985) study on marine iguanas revealed that female site preference is linked at least in part to the site's thermal properties, which influence the mating success of resident males. In all of these studies, the thermally selected sites were completely distinct from remote feeding areas, a condition that is atypical of many terrestrial ectotherms, for which movement and territory decisions must be made amidst a mosaic of patches that differ in thermal properties and food quality. I examined the movements and social structure of the desert iguana (*Dipsosaurus dorsalis*), with the goal of assessing the relative importance of food and temperature in determining patterns of mating success in a patchy environment.

Dipsosaurus dorsalis ranges throughout the low-elevation deserts of the southwestern US, in habitats that are thermally heterogeneous, with patches of shade from shrubs providing relief from seasonally extremely high temperatures in the open. Unlike many other desert ectotherms, *D. dorsalis* remains active at midday during the hottest times of the year, using shade patches as thermal refuges to maximize aboveground activities such as territory defense and mating (Norris 1953; DeWitt 1967*a*). Since it is entirely herbivorous (Mautz & Nagy 1987), the sources of shade in the environment may double as the main sources of food. However, shrubs differ not only in their quality as food sources (Minnich and Shoemaker 1970; Porter *et al.* 1973), but also in the quality of shade they provide, due to species-specific differences in growth form (Hillard 1996). Except in the provident case of a single, common shrub species providing both high-quality food and optimum-temperature microclimates at midday, the maximization of territory quality in *D. dorsalis* will rely on a trade-off, in which the relative importance of the two resources are weighed. I tested the hypothesis that the social system and territory distribution of *D. dorsalis* is most closely dependent on the thermal properties of shrubs, with food sources being a less important factor in determining patterns of mating success. This hypothesis suggests the following predictions: (a) lizard home range distribution should correspond most closely with low temperature patches, rather than high-value food patches; (b) low temperature patches should be the focal points for mate competition among males; and (c) the most reproductively successful males should be those whose territories include the low temperature microsites. Lastly, to examine some of the sexually-selected consequences of this mating system, I quantified patterns of sexual dimorphism in this species and related those patterns to male dominance and the nature of resources defended by males.

METHODS

Study Area

In March 1994, I established a 1.7 ha study site near the intersection of Ogilby Road and I-8 in Imperial County, California (32°45.4 N and 114°50.2 W; elevation approx. 90 m). The site consists of a series of stabilized sand dunes interspersed with gravel-sand flats, on which most of the vegetation occurs. *Larrea tridentata*, *Ambrosia dumosa*, *Stephanomeria pauciflora*, *Eriogonum deserticolum*, and *Psorothamnus emoryi* are the dominant permanent shrubs, with smaller numbers of large, widely scattered *Chilopsis linearis* and *Olneya tesota*. The site receives an average 7.67 cm of precipitation annually, most of which falls during midwinter and late summer (U.S. Weather Bureau station in Yuma, AZ). I was on the site from 11 March - 17 May 1994, and 7 April - 1 June and 29 June - 10 July 1995, for a total of 132 d. During both years of the study, the early spring weather (March - early May) was unusually cool and cloudy.

I established a 10 x 10 m grid of flags on the site and mapped the location of all perennial plants with a canopy diameter of 50 cm or greater. To characterize the spatial distribution of shrubs, I counted the number of mapped shrubs in each 10 x 10 m grid square and calculated Morisita's (1962) index of aggregation (I_M) for each species. The I_M index measures how many times more likely it is that two randomly selected individuals will be from the same quadrat than it would be if all individuals were distributed randomly (Hurlbert 1990).

To quantify the availability of different plant species, I relied on three random sampling techniques, each with its peculiar biases. *Method 1*: I counted and measured (canopy diameter to the nearest cm) all living plants with a diameter of > 5 cm on nine 100 m^2 subplots, evenly spaced across the site (Fig. 1). While offering exact measurements and including all plant species within the subplots, this technique is biased by subplot location, since plant distribution was not uniform on the site and some plants (especially *A. dumosa*) were underrepresented in this sample. *Method 2*: I noted the plant cover (if any) on 562 microsites scattered in a grid pattern across the study site (Fig. 1). The western extreme of the study site was sampled with this method more thoroughly than the eastern end, which reflects the generally higher number of behavioral observations made in the western end. This method is limited by the small number of microsites (41) that had plant cover. *Method 3*: I counted all permanent shrubs on the entire study area with a canopy diameter > 50 cm, which neglects small plants but equally represents all portions of the study area and is a useful measure of the most important sources of shade.

In calculating the cover area for annuals, I relied exlcusively on the subplot counts (Method 1, above). To calculate cover area for the six species of permanent shrubs (*A. dumosa, C. linearis, E. deserticolum, L. tridentata, P. emoryi*, and *S. pauciflora*), I used the averaged results of the three methods described above to assign a relative abundance to each of these six species. These new relative abundance indices were then used to reallocate the total cover from the subplot measurements (Method 1) that was not occupied by annuals. The combination of several methods in calculating shrub area balances the biases inherent in each method, and increases the likelihood of ranking the six shrubs correctly.

I attempted to capture every adult *D. dorsalis* on the site, although in 1994 a small number (< five) of large individuals remained unmarked. I did not attempt to mark 1 to 2 year old individuals, which are generally distinguishable from reproductively mature adults by size alone. Reproductive maturity in this species is attained after 3 - 5 years (Mayhew 1971, Krekorian 1984). Lizards were noosed or captured with wire mesh live traps baited with carrot shavings; I captured 60 lizards in 1994 and 67 in 1995 (for recaptures see below). For noosed lizards, I recorded body temperature (T_b, measured cloacally) and substrate and air temperatures (T_{sub} and T_{air}; shaded thermocouples buried slightly, and held 2 cm above the substrate, respectively) at the site of capture with a quick-reading thermometer (Miller-Weber® Inc., Queens NY, USA) or a thermocouple thermometer (Digi-sense® model 8528-10, Cole-Parmer, Niles IL, USA). I then measured the following on each individual (head measurements taken with digital calipers to the nearest 0.1mm):

-snout vent length (SVL), taken with a straight ruler to the nearest mm

-mass to the nearest g, using a 300g Pesola spring scale

-head width at the widest point on the head (HW1)

-head width at the outer edges of the supraocular scales (HW2)

-head length from the anterior edge of the ear opening to the tip of the rostrum (HL)

-head height from the parietal eye to the gular area (HH1)

-head height from the upper edge of the supraocular to the jawline, at the level of the eye (HH2)

For each head dimension, I took the average of three to five separate measurements (more measurements were taken when the variation between measurements was higher; sequential measurements generally fell within 0.03 mm of each other). In measuring HW1 and HH1, I closed the calipers to the point that resistance was felt. I marked each individual with colored 4-mm glass beads strung on surgical steel and sewed to the tail (Fisher & Muth 1989). All individuals were processed immediately after capture and as quickly as possible (maximum process time 15 min). During the second year of fieldwork, I recaptured 10 individuals of known identity and nine individuals with scars on the tail where the bead tags had come loose. Those in the latter group were retagged, but were excluded from morphological analyses since they represented recaptures of unknown identity. For the 10 recaptured lizards of known identity, I used morphological data from the second year only in the analyses.

To examine allometric differences in morphology among groups, I analyzed the residuals of the overall regression between body length and the variable of interest. This allowed me to examine morphological differences among groups independent of body size.

Behavioral Sampling and Home Range Designation

I used several methods to compare behaviors and space use patterns among groups of lizards. To construct time budgets, I took 115 detailed focal samples of 15 females and 29 males (total time = 24.7 h; $\bar{x}$ time per sample = 12.9 min). Each focal sample included the following data:

Exposure - I recognized the categories sun, shade, and partial shade (psh), which includes dappled shade or diffuse light filtered through vegetation. I also noted the species of shrub providing shade.

Behavior Category - I recognized eight categories that included all continuous behaviors observed:

Stationary - basking/nonmoving; for this category, I also noted whether exposure was sun, psh, or shade, and which plant served as shade source.

Move - any movement that lasts longer than three seconds.

Feed - feeding on vegetation; this category includes the brief movements made as the animal feeds; e.g., climbing through a shrub and feeding simultaneously.

Court - courtship begins when a male approaches a female and initiates a characteristic, low-amplitude head movement termed vibratory head-nodding (Distel & Veazy 1982; also equivalent to Dugan's [1982] "shudder bob") that is distinct from the pushup display (see *display rate*, below). A typical courtship includes bouts of vibratory head-nodding separated by pauses; if the pauses were shorter than 5 minutes, I recorded the entire sequence, including pauses, as courtship.

Chase/Fight- chases include all encounters whether the focal individual is the chaser or is being chased.

Interaction - brief pauses during intrasexual encounters (e.g., stand-offs involving two displaying individuals).

Location - the individual's location on the scale map (when not moving).

Display Rate - the number of pushup displays ("signature bob;" Carpenter & Ferguson 1977).

During each sample, I noted the time of any change in location, exposure, or behavior category; thus, the focal sample provides a continuous record of animal activity. To compare time budgets between groups, I averaged the results of all focal samples for each individual lizard. To examine the time budget as a function of season or time of day, however, I treated each focal sample as a statistically independent event. Although there may be inherent differences among individuals and, thus, nonindependence of subsequent samples on the same individual, this method examines whether season or time of day effects are strong enough to still be apparent on the same individual over time.

To examine temporal patterns of activity, I conducted 80 "walking censuses," distributed across all months of the study and all hours of the day from 0800 to 1700. In each census, I walked the entire site in a zigzag fashion for 30 min, locating animals with binoculars, and noting the exposure and behavior category of each sighted *D. dorsalis* (marked or unmarked). In addition to focal samples and walking censuses, I spent approximately 42 h seated in areas that afforded a wide view (typically at the crest of a dune) from which I could scan a number of lizard home ranges with binoculars. This technique yielded an increased sample size of rare behaviors, including courtships and copulations, chases, and territory incursions. These samples were further augmented by opportunistic observations taken during plant surveys or other activities while on the site.

I used location data from the walking censuses and opportunistic resightings of marked animals to designate home ranges with the minimum polygon method. Most *D. dorsalis* have small home ranges, typically with a cluster of sightings around a particular shrub; others have larger, more dispersed home ranges with no clear center of activity. I designated a particular shrub as an individual's home range center (HRC) if 50% or more of the sightings were beneath the shrub or within 2 m of its edge.

Thermal Measurements

Throughout 25 days during the 1995 season I sampled microhabitat temperatures beneath the six permanent shrub species, as well as in the open. Except for unusually large individuals of *Palafoxia linearis* and *Asclepias subulata*, these six shrubs were the only plants capable of providing full shade exposure to an adult lizard. I used bare thermocouples, shallowly submerged beneath the sand to record T_{sub} and elevated 2 cm to record T_{air}. Thermocouples in the open were shaded. I used a 5-channel OMEGA® datalogger (Omega Engineering Inc., Stamford, CN, USA) to sample five microhabitats at 15 min intervals simultaneously, moving thermocouples daily to represent as many individual shrubs as possible. During the June-July 1995 sample, equivalent temperatures were taken at hourly intervals with bare-bulb Miller-Weber® thermometers (shaded when in the open). To examine the effects of shrub species on shade temperature, I restricted my analyses to those days in which the day's high temperature (measured in the shade of an *Olneya tesota* tree, at a height of 1 m) exceeded 30°C and used repeated measures ANOVAs on T_{sub} and T_{air} of each shrub species to factor out the effect of time; the microhabitat "open" was excluded from these analyses to restrict comparisons to among shaded microhabitats. Separate analyses including open microhabitats revealed that all plants were significantly cooler than open microhabitats (Scheffe multiple comparisons $p < 0.0001$).

In July 1995, I conducted a tethering experiment to determine the relationship between shrub temperature and lizard T_b. I tethered 10 adults with a 1-m long string beneath the shade of each of the five most widely available shade sources (*E. deserticolum, L. tridentata, S. pauciflora, P. emoryi,* and *A. dumosa*). These experiments took place between 0830 and 1200 h, during the normal time of lizard activity. For each trial, I allowed 10 min for the lizard's T_b to respond to the microclimate, then immediately measured T_b (cloacally), T_{sub} and T_{air}. Although the tethered lizard was free to move within a 1 m radius beneath the shrub and into sun exposure, most lizards moved little during the trials; typically they briefly explored the environment before remaining motionless. The trial was terminated immediately if the lizard began panting, indicating a T_b approaching 43 °C, which is close to the lethal limit (DeWitt 1967*b*); this occurred in five of the ten *E. deserticolum* samples and four of the ten *P. emoryi* samples, since these shrubs provide relatively poor shade cover. Thus, end T_b's for these two shrub species are underestimates. The order of shrubs tested was randomized for each lizard, although I did not run *P. emoryi* and *E. deserticolum* in sequence, which would have subjected animals to long periods of excessive temperatures.

Determination of Male Dominance

I observed 42 interactions involving marked male-male pairs in which I could clearly designate a winner and loser, including 39 chases and three contact fights. Based on these observations, I ranked males as follows: ***dominant*** males were those that chased or supplanted other males and were never themselves chased; ***subordinate*** males were chased but were never observed chasing another male; ***mid-rank*** males were chased by dominant males, but chased subordinate males. Males that were never observed in agonistic encounters were not ranked. Within the ranked males, reversal of dominance only occurred with one pair of males that seemed co-dominant in the vicinity of the *C. linearis* in 1994; on three separate occasions they engaged in full lateral displays followed by chases, and each male was victor at least once. I designated both of these males as dominant, since both also chased a number of other males from the shrub. Altogether I ranked 16 males as dominant, five as mid-rank, and nine as subordinate. For some analyses, I lumped the latter two groups as "low rank."

Courtship Behavior and Female Response

I observed 101 courtship events in which the entire sequence was visible (28 of the courtships were from focal samples; the remainder were from walking censuses and other opportunistic sampling). Courtships begin when the male approaches the female and initiates vibratory head-nodding, then proceed with the male grasping the female's neck in his jaws prior to copulation. There may be several bouts of head-nodding separated by brief pauses, and the sequence can be terminated during any stage. For each courtship sequence I timed the events and categorized the behaviors that caused the cessation of courtship as follows: (a) *female leaves*; the female moves more than 3 m or makes herself unavailable, such as running down a burrow; (b) *female chased*; the female is chased by another male or by the courting male; (c) *male chase*; the male is chased by another male or chases another male; (d) *male courts another*; male ceases courting to court a different female; (e) *male stops*; the male ceases head nodding even though the female has responded minimally. Of the eight sequences in which the neckgrab was attained, I classified four as "female resistance" because the female struggled violently, and in each case managed to escape the male. I treated each courtship as a statistically independent event, analyzing time spent courting with t-tests on dominant vs. low-rank males, and analyzing courtship outcomes via a contingency table analysis. Treating all courtships as independent events increases the sample size and, thus, the likelihood of finding a significant male status effect (but see Results).

All data analyses were conducted with Statview IV (Abacus Concepts 1992). Plant names follow Hickman (1993).

RESULTS

Plant Availability and Thermal Ecology

Like most sites in the lower Colorado Desert, the majority of the study site was barren of vegetation, with 5.0% plant cover (derived from averaging the results of vegetation census Methods 1 and 2). Over half of the plant cover on the site is occupied by permanent shrubs, with *E. deserticolum* dominating (Table 1). The dominance of the next most common plant, the annual herb *Caulanthus pilosus,* is mitigated by the fact that by early May, this species has generally withered and dried to the point of no longer providing shade or forage for lizards. The rarest shrub was *C. linearis*, of which a single large individual was present. The largest plants on the site were some individual *L. tridentata* and the *C. linearis*, which exceeded 3 m in crown diameter; however, all species of permanent shrubs were represented by several individuals with crown diameters exceeding 2 m. Shrubs were unevenly distributed on the site, with the highest densities for most species being in the western third of the site (Fig. 2). *Eriogonum deserticolum* and *L. tridentata* were the most evenly distributed across the site (I_M = 2.66 and 3.13, respectively), *S. pauciflora* and *A. dumosa* were the most aggregated (I_M = 7.03 and 6.57, respectively) and *P. emoryi* was intermediate (I_M = 4.86).

Temperature profiles for spring (mid March - late May) and summer (late June - early July) reveal that substrate temperature varied more among microhabitats than air temperature (Fig. 3). In the spring, the effect of shrub species was significant both on T_{air} (repeated measures ANOVA, $F_{1118,16,3} = 51.971$, $p < 0.0001$) and T_{sub} ($F_{563,16,3} = 102.529$, $p < 0.0001$). There was no significant shrub*time interaction for either T_{air} or T_{sub} (p = 0.759 and 0.340), indicating that shrub species do not differ in their temporal pattern of warming or cooling. In the summer there is a significant shrub effect on T_{sub} ($F_{40,10,4}$ = 22.5, p = 0.0053) but no shrub effect on T_{air} ($F_{40,10,4} = 3.22$, p = 0.182) and no shrub*time interaction on either T_{sub} (p = 0.085) or T_{air} (p = 0.241). Multiple comparisons revealed many between-shrub differences (Table 2), with a general trend for *E. deserticolum* and *P. emoryi* to have the highest temperatures and *L. tridentata* and *C. linearis* to have the lowest (see Fig. 3).

The mean T_b of noosed *D. dorsalis* was 39.47 °C ± 0.154 SE (range: 35 - 42.5 °C). The mean environmental temperature taken at the capture site ($(T_{air} + T_{sub})/2$) was a better predictor of lizard T_b than either microhabitat measure alone (Fig. 4; regression equation for T_{air}: $Y = 35.32 + 0.118 X$, $r^2 = 0.199$, $p = 0.0056$; T_{sub}: $Y = 36.70 + 0.07 X$.

$r^2 = 0.069$, $p = 0.115$). Most lizards were captured away from shrubs, or moved through a mix of sun and shade prior to capture, making a comparison of noosed T_b among plant types impractical. The results of the tether experiment, however, reveal a significant shrub effect on T_b (ANOVA, $F_{45,4} = 6.333$; $p = 0.0004$; Fig. 5, Table 3). Lizards tethered beneath *P. emoryi* and *E. deserticolum* had higher T_b's than after being tethered beneath *L. tridentata* (Scheffe multiple comparison $p = 0.0223$ and $p = 0.0380$, respectively). Lizards tethered beneath *Stephanomeria pauciflora* were the second-coolest, and were significantly cooler than lizards under *P. emoryi* (Scheffe $p = 0.0322$) but only marginally cooler than those under *E. deserticolum* (Scheffe $p = 0.0537$). The T_b's reported for lizards under *E. deserticolum* and *P. emoryi* are underestimates, since many of the tether samples under these two shrubs were truncated due to signs of temperature stress in the lizards (see Methods). Comparisons of the mean environmental temperatures ($(T_{air} + T_{sub})/2$) of the shrubs revealed the same significant differences that the T_b tests showed, in addition to which the following shrub pairs differed significantly: *A. dumosa - E. deserticolum*; *A. dumosa - P. emoryi*; and *S. pauciflora - E. deserticolum* ($F_{45,4} = 8.641$; $p < 0.0001$; Scheffe multiple comparisons, $p < 0.05$).

Activity Patterns and Habitat Use

This population exhibited a generally unimodal activity pattern, with activity times earlier in the day during the summer months (Fig. 6). The number of lizards seen per minute varied with time of day (repeated measures ANOVA with time and season as factors; $F_{83,8,1} = 3.069$, $p = 0.024$), and there is a marginally significant interaction between time and season ($F_{83,8} = 2.009$, $p = 0.0619$), indicating that the pattern of daily activity tends to differ between spring and summer. Walking censuses indicated that patterns of sun and shade exposure vary as a function of time of day (Fig. 7), with a trend toward decreasing sun exposure later in the day (repeated measures ANOVA with time and % sun exposure as factors; $F_{65,8} = 2.38$, $p = 0.0397$) and a simultaneous increase in shade exposure ($F_{65,8} = 2.882$, $p = 0.0186$). There was also a significant trend for reduced psh exposure and increased shade exposure in the summer compared to the spring (ANOVA with season as a factor, time of day not included; $F_{87,1} = 5.666$, $p = 0.0195$ and $F_{87,1} = 37.362$, $p < 0.0001$, respectively). Sun exposure, however, did not vary seasonally ($F_{87,1} = 2.470$, $p = 0.1197$). There were no differences in the frequency of use of different shrub species between spring and summer (ANOVAs on % shrub use with season as factor; p value range 0.136 - 0.662).

Focal samples revealed that both male and female *D. dorsalis* spend much time stationary, usually in sun or psh exposure (Table 4). The small percentage of time spent moving was generally occupied by frequent, brief moves, with the end result being a shuttling between sun and psh or shade. In general, activity patterns of males and females are similar; however, males utilized the pushup display more often.

Dipsosaurus dorsalis in this population are extremely catholic in their diet, feeding at least occasionally on almost all the plant species on the study site (Table 1). Of the 118 observed feeding events, 50 were on one of the six permanent shrub species. The most important foodplants were *S. pauciflora* (flowers), the herbaceous *Tiquilia plicata* (leaves), and *P. emoryi* (both flowers and leaves); in contrast, the two most abundant permanent shrubs (*L. tridentata* and *E. deserticolum*) were among the least used food sources. Figure 8 combines data on relative cover, feeding frequency, and shade use for the six permanent shrub species. Shrubs disproportionately selected as food sources included *S. pauciflora, P. emoryi*, and *C. linearis*. In contrast, those disproportionately selected as basking sites included *L. tridentata*, *C. linearis*, and, to a lesser extent, *A. dumosa*.

Male Dominance, Home Range, and Mating Success

Both male and female *D. dorsalis* exhibit intrasexual aggression; however, most escalations (e.g., full chases) were between male-male pairs. Males in this population maintain a 2-step dominance hierarchy. Dominant males use the pushup display more often than do low-status males (mid-rank and subordinate males lumped; t-test, $t_{20} = 4.411$, $p = 0.0003$), but otherwise, patterns of exposure, movement rates, and behavior categories are similar (t-tests on focal sample data; p value range 0.07 - 0.785).

Fights were relatively rare (six observed, three of which were between marked individuals), and followed extended lateral displays in which both males circled and headbobbed. After displaying, the pair would approach and bite one another's forelimbs or thighs and, while maintaining this mutual jaw-lock, would slap each other with their tails. Fights rarely lasted more than three minutes, during which there were usually several bouts of biting and tail-slapping separated by brief pauses.

A large proportion of female home ranges were associated with large shrubs, particularly *L. tridentata* and *C. linearis* (Table 5); however, some individual females also had widely dispersed home ranges with no definable HRC (Fig. 9A). This pattern is generally mirrored by the distribution of male home ranges/territories. The areas of highest female home range overlap (in particular, the *C. linearis* and a number of *L. tridentata* in the western half of the study area) formed the nuclei of dominant male territories (Table 5, Fig. 9B), whereas low-rank males often had no definable HRC, and their activity areas tended to be larger than those of dominant males.

Courtships on the study site were more highly clumped in space than were feedings, as revealed by the Morisita index of aggregation (Fig. 10). There were no obvious "hotspots" of feeding activity, but there were clearly sites, such as the *C. linearis* and a few *L. tridentata*, at which a number of courtships took place.

Males whose territories centered on either *L. tridentata* or *C. linearis* courted a greater number of females than males with home ranges/territories centered on other shrub species or those with no definable home range center (ANOVA on # of females courted, with shrub species as a factor; $F_{23,5} = 2.645$, $p = 0.0497$; Fig. 11). However, there were no concomitant effects on male behavior, as evidenced from focal samples. Exposure, movement rates, feeding rates, and courtship rates were not influenced by shrub (ANOVAs on focal data with shrub HRC as a factor, p value range 0.065 - 0.731).

Courtship Behavior

Very few courtship events terminate in copulation; in fact, only eight (7.92%) of the observed 101 courtship events reached the neckgrab stage (Fig. 12). The two most common causes of courtship termination are the male stopping (N = 37; 36.63% of all courtships) and the female leaving (N = 34; 33.66%). Male-male interactions are also an important factor; males frequently end the courtship to chase another male (N = 9; 8.9%) or are themselves chased away from the female (N = 4; 3.96%). Females resisted four of the eight neckgrabs; of these, three females escaped on their own and the fourth escaped when the courting male was chased by a dominant male. The remaining four neckgrabs terminated in copulation; in none of these was female resistance of any kind observed.

Males of different status did not court females differently. Dominant males and low-rank males courted for the same duration of time, whether measured as time spent head-nodding (t-test, $t_{34} = 1.688$, $p = 0.1005$), number of head-nodding bouts involved in the courtship ($t_{100} = 0.517$, $p = 0.6066$), or total duration of courtship, including head-nodding time and pauses between bouts ($t_{27} = 1.254$, $p = 0.2206$). Similarly, male status did not significantly affect the nature of courtship termination; all males were equally likely to stop courting on their own, and female response did not differ as a function of male status (Chi-square on courtship outcome with male status; contingency coefficient $= 0.262$, $p = 0.2599$).

Sexual Dimorphism

This population of *D. dorsalis* is sexually dimorphic, with males being proportionately larger in all measurements except mass (t-tests on residuals of the overall regression with log BL; $p < 0.01$). Separate regressions of HL, HW2, and HH2 for males and females are shown in Fig. 13.

Among males, there are significant differences between dominant and subordinate males in HL (ANOVA, $F_{2,27} = 6.104$, $p = 0.0065$; Scheffe multiple comparison $p = 0.0076$) and HW2 ($F_{2,27} = 4.218$, $p = 0.0255$; Scheffe $p = 0.0276$), and mid rank males differ significantly from subordinate males in HH1 ($F_{2,27} = 4.220$, $p = 0.0254$; Scheffe $p = 0.0381$). However, there are no differences between dominant and mid-rank males

(Scheffe $p > 0.05$). Also, there are no differences among males in proportionate head size (low-status males grouped; Fig. 14).

Male size differed among shrubs; males whose HRC was *L. tridentata* or *C. linearis* had significantly longer bodies than those whose territories centered on *E. deserticolum* or who had no HRC (ANOVA, $F_{26,6} = 5.861$, $p = 0.0006$, Scheffe multiple comparisons $p < 0.05$). Also, males whose HRC was beneath *L. tridentata* and *C. linearis* had longer heads than those who had no HRC ($F_{26,6} = 5.623$, $p = 0.0008$, Scheffe multiple comparisons $p < 0.05$). Males whose HRC was beneath *L. tridentata* were also significantly heavier than males with no HRC (ANOVA, $F_{26,6} = 5.342$, $p = 0.0010$). However, residual analyses indicated no differences among these males in head-body proportions (HL: $F_{26,6} = 1.269$, $p = 0.3057$; HW1: $F_{26,6} = 0.669$, $p = 0.6753$; HW2: $F_{26,6} = 1.245$, $p = 0.3164$; HH1: $F_{26,6} = 0.802$, $p = 0.5771$; HH2: $F_{26,6} = 2.243$; $p = 0.0707$). Thus, males with territories centered on the coolest two shrub species (*L. tridentata* and *C. linearis*) had longer bodies and absolutely longer heads but were not proportionately larger-headed.

DISCUSSION

Food availability, predator escape, and social influences are generally considered to be primary determinants of movement patterns and space use for most animals (Emlen & Oring 1977 [see Davies 1991 for review]). In *D. dorsalis*, a complex system of home range placement and mate acquisition results from spatial and structural limitation of thermally acceptable microclimates. Thus, the mating system of this species is influenced by the physiological consequences of habitat use (Huey 1991).

The Biophysical Environment and Lizard Activity

I used measurements of T_{sub} and T_{air} to serve as surrogates for T_e (operative temperature) measurements, which have traditionally been taken with copper models (Bakken, Santee, & Erskine 1985; Bakken 1992). Operative temperatures predict the endpoint T_b for a nonthermoregulating animal, and copper models have the advantage of being insensitive to the relative roles of solar radiation and air temperature in determining T_b, because the influences of these factors change with time of day and wind conditions (Bakken 1992). However, in this study insolation is a relative unimportant factor because comparisons were made primarily among shaded microhabitats. Moreover, the specific question addressed by measurements of T_{air} and T_{sub} is whether some microhabitats are unsuitable for the specific reason of not allowing lizards to attain T_b within an acceptable range (using the observed range of T_b for noosed lizards at this site--35 - 42.5 °C--as a baseline) during normal activity periods. The lizard tethering experiment serves an acceptable substitution for T_e models in this context, because variation in $(T_{air}+T_{sub})/2$ explained 89.5% of the variance in lizard T_b (Figure 5); this calibration is comparable to that of T_e model studies (e.g., Peterson 1987; Grant & Dunham 1988).

Microclimates vary with shrub species, with *L. tridentata* and *C. linearis* having the lowest measured environmental temperatures and *E. deserticolum* and *P. emoryi* having the highest. This same trend is supported by the tether experiment data, which reveal a significant shrub effect on lizard T_b and a tight relationship (r^2 = 89.5%) between environmental temperature and T_b (Fig. 5). The coolest shrub microclimates are provided by shrubs with a large, closed canopy and few branches at ground level, allowing unimpeded air flow at the base of the plant. In the Mojave Desert, *A. dumosa*, a shrub with a dense network of branches at ground level, actually had higher T_e than adjacent open areas with full sun exposure but unimpeded air flow (Hillard 1996). I found that *A. dumosa* tended to lose heat more slowly in the late afternoon than other shrubs (Fig. 3, spring), possibly as a result of this boundary layer effect. This may have influenced the results of the tether experiments, which were conducted in the morning (the normal activity period during the summer).

Dipsosaurus dorsalis begins its annual activity cycle in late February to mid-March, with juveniles emerging before adults (*personal observation*). The observed seasonal shift in activity times, with lizards emerging earlier during the hotter months (Fig. 6), conforms to a temperature-based prediction of activity pattern. At all times of the year, the daily activity begins with a "warm up" basking period in open sun. Access to heat is generally not limiting at the study site, because bare ground with full sun exposure is ubiquitous on the study site (as it is in all habitats selected by this species). The sites expected to allow the most rapid heating are south-facing slopes such as dunes, where substrate heating should be maximized, or sites on the sunny side of shrubs, which have higher operative temperatures owing to increased thermal reflectance from the shrub (Hillard 1996). After the morning warm-up, lizards shuttle between sun and psh microhabitats, resulting in approximately equal use of each (Fig. 7) until the afternoon, when shade habitats are frequently used before the animals retreat into burrows. Aside from a small peak of activity in late afternoon in the summer (Fig. 6), there was no evidence for a bimodal activity period. *Dipsosaurus dorsalis* in the Mojave Desert of southern California also show a unimodal activity period, *contra* the predictions of models based solely on temperature (Porter *et al.* 1973). Clearly, other considerations besides temperature must play a role in determining animal activity patterns. Minimizing exposure to high environmental temperatures may be expected in times of low food availability, when energy needs to be conserved (e.g., Zimmerman & Tracy 1989) or if hydric costs of high T_b exceed the benefits of increased activity time.

The mean T_b of noosed *D. dorsalis* (39.47 °C) is higher than the mean reported in laboratory thermal gradients (38.5 °C, DeWitt 1967*b*; 39 °C, McGinnis & Dickson 1967), but lower than T_b means reported for other free-ranging populations (e.g., 42.1 °C, Norris 1953). The set point temperature (T_{set}, sensu Hertz, Huey, & Stevenson 1993) for *D. dorsalis* most likely lies between 38 and 40 °C (DeWitt 1967*a*, 1967*b*). However, various ecological and social factors may cause the animal to "abandon" set point temperatures, as for the iguanid *Conolophus pallidus*, which tolerates T_b below T_{set} to maximize the time during which a stable T_b can be maintained (Christian, Tracy, & Porter 1983). *Dipsosaurus dorsalis* has been hypothesized to tolerate excessively high environmental temperatures as a cost of maintaining aboveground activity, (DeWitt 1967*a*; Porter *et al.* 1973), with individuals exhibiting "voluntary hyperthermia" T_b's of 44 - 46 °C (Norris 1953; Porter *et al.* 1973). However, while this tolerance range may allow lizards to move through a mosaic of thermal patches, including open sun and high-temperature shrubs such as *E. deserticolum* and *P. emoryi*, many of these microhabitats would be lethal to the animals, given extended exposure times. Hence, although *D. dorsalis* can briefly tolerate high temperatures, occasional retreats (i.e., access to cool-temperature shrubs or to burrows) are required.

Dipsosaurus dorsalis spends a very small portion of its time budget feeding (Table 4), possibly a result of the relatively low energy needs of an ectothermic metabolism, coupled with a diet rich in flowers, which have a higher digestible fiber content than do leaves (Mautz & Nagy 1987). Other studies (Norris 1953; Minnich and Shoemaker 1970) have shown a similar predominance of flowers in the diet, but the complete absence of any feeding on *L. tridentata* is unusual; this plant is widely regarded as one of the primary food sources for this lizard (Norris 1953, Stebbins 1985; Mautz & Nagy 1987). Perhaps the local availability of *S. pauciflora* flowers lured the animals away from the flowers of *L. tridentata*, which were available and abundant during both spring seasons.

Social System and Home Range

Although males exhibit a clear two-step dominance hierarchy, overall levels of aggression are lower than reports for other iguanids (e.g., *Sauromalus obesus*, Berry 1974; *Ctenosaura pectinata*, Evans 1951; *C. hemilopha*, Carothers 1981). Dominant males were usually the most easily observable members of the population, perched in a prominent location from which they chased other males that encroached on their territory. The lower rate of pushup displays by low-rank males is in keeping with their generally inconspicuous nature, and typical of "sneak copulator" strategies observed in other polygynous systems (e.g., Gerhardt *et al.* 1987). Female-female aggression was commonly observed, but unlike males, females tolerate the close proximity of other members of the same sex, and thus overlap of female home ranges was greater than for males. This social arrangement sets the stage for some degree of mate monopolization by males.

Female home range overlap was highest beneath the canopy of large *L. tridentata* and the lone *C. linearis* (Fig. 9A), and although the chief areas of female overlap were under the control of dominant males, several other dominant males had territories centered on relatively small shrubs (albeit usually *L. tridentata*). This distribution seems to be a reflection of female site choice, with male territories apparently more closely tied to patterns of female home range overlap and not exclusively to the presence of large shrubs. Several large *L. tridentata* had no resident females, and several females ranged widely over large areas, using a mixture of small shrubs rather than centering their home ranges on a single one. The absence of any clumping pattern in the distribution of feeding events eliminates the possibility that wide-ranging males are defending feeding "hotspots," but they may be responding to the movements of the few wide-ranging females. Perhaps my emphasis of the thermal properties of shrubs in determining home range quality is an oversimplification, and the alternative strategy of a larger home range encompassing a number of shrub species may offer equal home range quality. The notion of home range quality as a function of thermal properties has been explored (Waldschmidt & Tracy 1983; Tracy & Christian 1986; Huey 1991); clearly, home range quality will encompass a number of biotic and abiotic factors, and teasing them apart in unmanipulated systems may be difficult. Even in this relatively extreme environment, where many environmental temperatures are not only suboptimal but are lethal, not all individual lizards conform to predictions of home range placement based on a purely temperature-based model. However, the qualitative trends do support the notion that temperature, not food, exerts the stronger influence in determining site use among females and mating success among males.

Courtship Behavior

Because males appear to partition space according to status, with a preponderance of dominant males defending large, cool-shade shrubs as territories, one might hypothesize that courtship strategies and outcomes may vary either as a function of male status or as a function of the "quality" of a male's territory. Analyses of courtship times and outcomes suggest that this is not so. Males of all status spend equal amounts of time in the pre-neckgrab stages of courtship, and the frequency of outcomes does not differ among males. These results provide no evidence for the presence of female choice, but do not eliminate the possibility. Females may be exercising choice by selectively settling areas defended by particular males, selecting males rather than the physical aspects of a home range *per se*. However, two "natural experiments," in which dominant males died (one from presumed predation by the rattlesnake *Crotalus cerastes* and one from undetermined causes), leaving their territory to be taken over by low-rank males, suggest that female site use is not dependent on male identity. In both cases, female home ranges did not change as a result of male turnover, and the males that inherited the shrubs exhibited subsequent patterns of behavior (including pushup rate and courtship rate) similar to those of the former territory owners.

The overall rarity of observed copulations suggests that females do not engage in copulations with multiple males. Pre-oviposition females, with bodies distended with eggs, are rarely observed, and those females observed to copulate disappeared within 2 days of the event. Most likely, females copulate once and then go underground until oviposition. A dearth of females with oviductal eggs in museum collections (L. J. Vitt, *personal communication*) suggests that this is a general behavioral trend for the species. The presumed low incidence of multiple insemination possibilities has implications for the evolution of sperm competition among males (e.g., Olsson, Gullberg, & Tegelstrom 1994). In some species, multiple inseminations provide an access to reproductive success for low-rank males (see reviews in Birkhead & Hunter 1990; Birkhead & Moller 1992), for whom sneak copulations or even forced copulations may result in fertilizing some portion of the egg clutch. The rarity of copulations overall may thus intensify the disparity in reproductive success between dominant and low-rank males. However, in this system access to females and thus, to copulations, is not limited to high-rank males. Indeed, in the absence of evidence for female choice during courtship, and assuming a low incidence of multiple paternity for egg clutches, male reproductive success seems to rely heavily on home range placement, which will determine the number of females with which a male may potentially interact.

Sexual Dimorphism

The smallest iguanid, *D. dorsalis* is also one of the least sexually dimorphic (Carothers 1984). Sexual dimorphism in this family has been attributed to the effects of sexual selection, since food partitioning (one of the alternate causes of sexual dimorphism; Schoener 1967) has not been observed in any iguanid (Carothers 1984). The slopes of the regressions of body length versus head dimensions for males and females (Fig. 13) are more similar than those reported for other iguanids (e.g., members of the genus *Ctenosaura*; Evans 1951; Fitch & Henderson 1977; also see Carothers 1984) indicating lower sexual dimorphism in *D. dorsalis*. This suggests a lower level of intensity of selection on males for large head size than has been demonstrated for other iguanids. In general, the family Iguanidae is characterized by extreme levels of sexual dimorphism and intense local mate competition that results from the highly clumped nature of female burrows in many species (Dugan & Wiewandt 1982). The burrows of *D. dorsalis* are moderately clumped; the lizards either dig their own or use those of *Dipodomys* kangaroo rats (Norris 1953). Perhaps soil friability is a factor in determining the degree of burrow clumping in iguanids; in many species burrows are a limiting resource (e.g., Evans 1951; Carothers 1981; Case 1982; Wiewandt 1982), whereas in this population of *D. dorsalis* the widespread availability of sandy soil suitable for burrowing may offer more opportunities for burrow placement.

Male *D. dorsalis* use their heads as weapons in combat, similar to some phrynosomatids (e.g., Hews 1990) and scincids (e.g., Vitt & Cooper 1985), in which larger-headed males have an advantage in combat. For example, Hews (1990) found that head depth, and not head width or length, was a good predictor of the winner of encounters in a phrynosomatid whose fighting behavior is similar to that of *D. dorsalis*. Intense selection on male fighting ability may be accompanied by allometric differences in head size between dominant and low-rank males (e.g., *Ctenosaura similis*; Gier 1997). However, no such allometric dichotomy was found among male *D. dorsalis* of different rank (Fig. 14). Dominant males were simply longer-bodied and had absolutely larger heads, but did not differ in head-body proportions. Since body size is correlated with age in lizards, this suggests that dominant males are probably the oldest males, and that selection may act on rapid growth among males, rather than on head allometry *per se*.

Summary

The relative roles of thermal and food resources in structuring the social system and patterns of mating success in an herbivorous iguanid were investigated. Female home ranges were widely dispersed, but with two to four individuals overlapping in the vicinity of large shrubs. These shrubs therefore served as the focal point for local mate competition among males. The single most important variable in determining home range placement and subsequent patterns of mate access for males is the thermal property of the shrub around which individuals base their activities, although other variables may clearly be influencing the pattern of movements and activities. Although males exhibit a clear dominance hierarchy, males of different statuses do not court females differently and do not experience different courtship success rates (as measured by proportion of courtships that terminate in copulation). This suggests that territory placement, which determines the number of females with which a male courts, is an important determinant of a male's potential seasonal reproductive success. Patterns of sexual dimorphism reveal lower intensities of selection on head dimensions than in other members of the family Iguanidae, although selection on body size may be important.

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Table 1. Relative abundance of all plant species on study site, and percentage of feeding events (of a total 118 observed feedings) by *D. dorsalis*. Plants indicated with an asterisk (*) are permanent shrub species; those indicated as "R" (rare) were not detected in any of the random sampling techniques, and were represented by fewer than five individuals on the site. % Cover is a composite measurement that interpolates several cover estimation techniques (see Methods).

Plant	Family	% Cover	% Feedings
*Eriogonum deserticolum**	Polygonaceae	31.1	0.8
Caulanthus pilosus	Cruciferae	18.0	7.6
*Larrea tridentata**	Zygophyllaceae	12.3	0
Tiquilia plicata	Boraginaceae	9.0	13.6
unidentified	Compositae	6.0	5.9
*Stephanomeria pauciflora**	Compositae	5.2	27.1
*Psorothamnus emoryi**	Leguminosae	4.3	9.3
Euphorbia albomarginata	Euphorbiaceae	3.6	5.9
*Ambrosia dumosa**	Compositae	3.3	1.7
Palafoxia arida	Compositae	2.7	7.6
Oenothera deltoides	Onagraceae	2.6	5.1
Plantago insularis	Plantaginaceae	1.0	1.7
Astragalus sp.	Leguminosae	0.4	3.4
*Chilopsis linearis**	Bignoniaceae	0.2	3.4
Schizmus sp.	Poaceae	0.2	0.8
Cryptantha sp.	Boraginacea	0.1	1.7
Mentzelia pumila	Loasaceae	0.1	0.8
Camissonia claviformis	Onagraceae	R	2.5
Baileya pleniradiata	Compositae	R	0.8
Abronia villosa	Nyctaginaceae	R	0
Orobranche cooperi	Orobranchaceae	R	0

Table 2. Scheffe post-hoc multiple comparisons of environmental temperatures beneath shrubs for spring and summer. Significant differences ($p < 0.05$) are indicated as follows: $A_1 = T_{air}$, spring; $S_1 = T_{sub}$, spring; $S_2 = T_{sub}$, summer; none of the summer T_{air} comparisons were significantly different. Temperatures for *C. linearis* were not taken during summer.

	C. linearis	*E. deserticolum*	*L. tridentata*	*P. emoryi*	*S. pauciflora*
A. dumosa	A_1	S_1,S_2	A_1	A_1	A_1
C. linearis		A_1,S_1		A_1,S_1	
E. deserticolum			A_1,S_1,S_2	A_1,S_1	A_1,S_1,S_2
L. tridentata				A_1,S_1	
P. emoryi					

Table 3. Scheffe post-hoc comparisons of *Dipsososaurus dorsalis* T_b after being tethered for 10 min beneath each of five shrub species. Mean differences shown (critical difference = 2.697); * = $p < 0.05$.

	S. pauciflora	*A. dumosa*	*E. deserticolum*	*P. emoryi*
L. tridentata	0.13	0.42	2.80*	2.99*
S. pauciflora		0.29	2.67	2.86*
A. dumosa			2.38	2.57
E. deserticolum				0.19

Table 4. Results of 115 focal samples ($\bar{x}$ sample time = 12.9 min) on adult male and female *Dipsosaurus dorsalis.* Mean values are presented ± 1 SE. * = t-test significant at $p < 0.05$.

Category	male (n = 29)	female (n = 15)	total (n = 44)
Exposure			
%stationary, sun	29.34 ± 4.69	29.88 ± 7.52	29.53 ± 3.97
% stationary, psh	33.11 ± 4.99	42.12 ± 8.93	36.18 ± 4.47
% stationary, shade	14.42 ± 4.49	14.13 ± 7.12	14.32 ± 3.78
Movement			
% time moving	11.58 ± 2.10	7.44 ± 1.75	10.17 ± 1.53
# moves/min	0.39 ± 0.06	0.35 ± 0.08	0.38 ± 3.78
Behavior			
% interacting	1.04 ± 0.51	2.51 ± 1.48	1.54 ± 0.60
% chasing	0.30 ± 0.11	0.24 ± 0.15	0.28 ± 0.09
% courting	1.42 ± 0.49	0.88 ± 0.56	1.24 ± 0.37
% feeding	1.84 ± 0.64	2.80 ± 1.68	2.17 ± 0.70
# pushups/min	0.58 ± 0.09	0.24 ± 0.07	*

Table 5. *Dipsosaurus dorsalis* home range centers (HRC) for 1995 as a function of sex and male status. Designation of a shrub as the home range center indicates that > 50% of the sightings were beneath or within 2 m of the shrub; "none" indicates a dispersed site use pattern, with no clear center of activity. The shrub *S. pauciflora* was not the center of any home range.

Plant	# Female HRC	#Dominant male HRC	#Low-rank male HRC
A. dumosa	3	1	2
L. tridentata	9	7	1
E. deserticolum	1	0	2
C. linearis	4	2	0
P. emoryi	1	1	0
none	3	1	7

FIGURE LEGENDS

Figure 1. Protocol for vegetation sampling. The outline of the 1.7 ha study site is shown. with shaded zones indicating the nine 100 m^2 subplots in which all plants with a diameter of > 5 cm were counted and measured; total cover was calculated for each species (Method 1). The grid of dots indicates the locations of microsites on which plant cover (if any) was noted (Method 2); eight of these microsites yielded ambiguous cover categories, resulting in a final N of 562. Finally, all shrubs with a diameter of > 50 cm were mapped and counted on the entire study site (Method 3); a sample mapped subplot is shown in the "exploded" view. Calculation of the relative cover for the six shrub species relied on all three estimation methods.

Figure 2. Distributions across the study site (divided into 100 m^2 units) of individual shrubs exceeding 50 cm canopy diameter, with Morisita's index of aggregation (I_M) calculated from the number of shrubs occupying each 10 x 10 m grid square.

Figure 3. Air and substrate temperatures (°C) beneath six shrub species and in the open (means + SE), in spring (mid-March - late May) and summer (late June - early July). Data for spring only include days with a high shade temperature of $\geq$ 30 °C. Ambros = *A. dumosa*; Eriog = *E. deserticolum*; Larrea = *L. tridentata*; Psoro = *P. emoryi*; Steph = *S. pauciflora*; Chilop = *C. linearis*. Shaded area represents range of body temperatures of noosed *D. dorsalis* (equivalent for spring and summer).

Figure 4. *Dipsosaurus dorsalis* body temperature (°C) as a function of the mean environmental temperature ($(T_{air} + T_{sub})/2$) taken at the capture site. Dashed line represents isotherm.

Figure 5. *Dipsosaurus dorsalis* body temperature (°C) as a function of mean environmental temperature ((T_a + T_b)/2) taken after being tethered for 10 minutes beneath each of five shrub species. Dashed line represents isotherm. See Table 3 for multiple comparisons.

Figure 6. *Dipsosaurus dorsalis* activity levels (means + SE), measured as individuals observed per minute during walking censuses at different times of the day, during the spring (mid-March - late May) and summer (late June - early July). Absence of SE bars indicates a single sample.

Figure 7. Proportion of *Dipsosaurus dorsalis* observed in full sun, partial shade (psh), or full shade as a function of time. Data are from walking censuses (spring and summer data combined); means + SE presented.

Figure 8. Six shrub species arranged in descending order of % cover (calculated as a % of the total for these six species only), with the % of feeding events and shade use by *Dipsosaurus dorsalis* (shade use calculated from opportunistic or walking census observations of lizards using plants as psh or shade basking sites).

Figure 9. (A) the distribution of female *Dipsosaurus dorsalis* home ranges (minimum polygon method) in the western third of the study site, with all shrubs serving as home range centers (HRC) and all shrubs > 2 m in diameter shown. (B) the distribution of dominant male (solid line polygons) and low-rank male (dotted line polygons) home ranges over the same area as (A).

Figure 10. The spatial distribution of feeding events and courtship events by *Dipsosaurus dorsalis* across the study site, with Morisita's index of aggregation

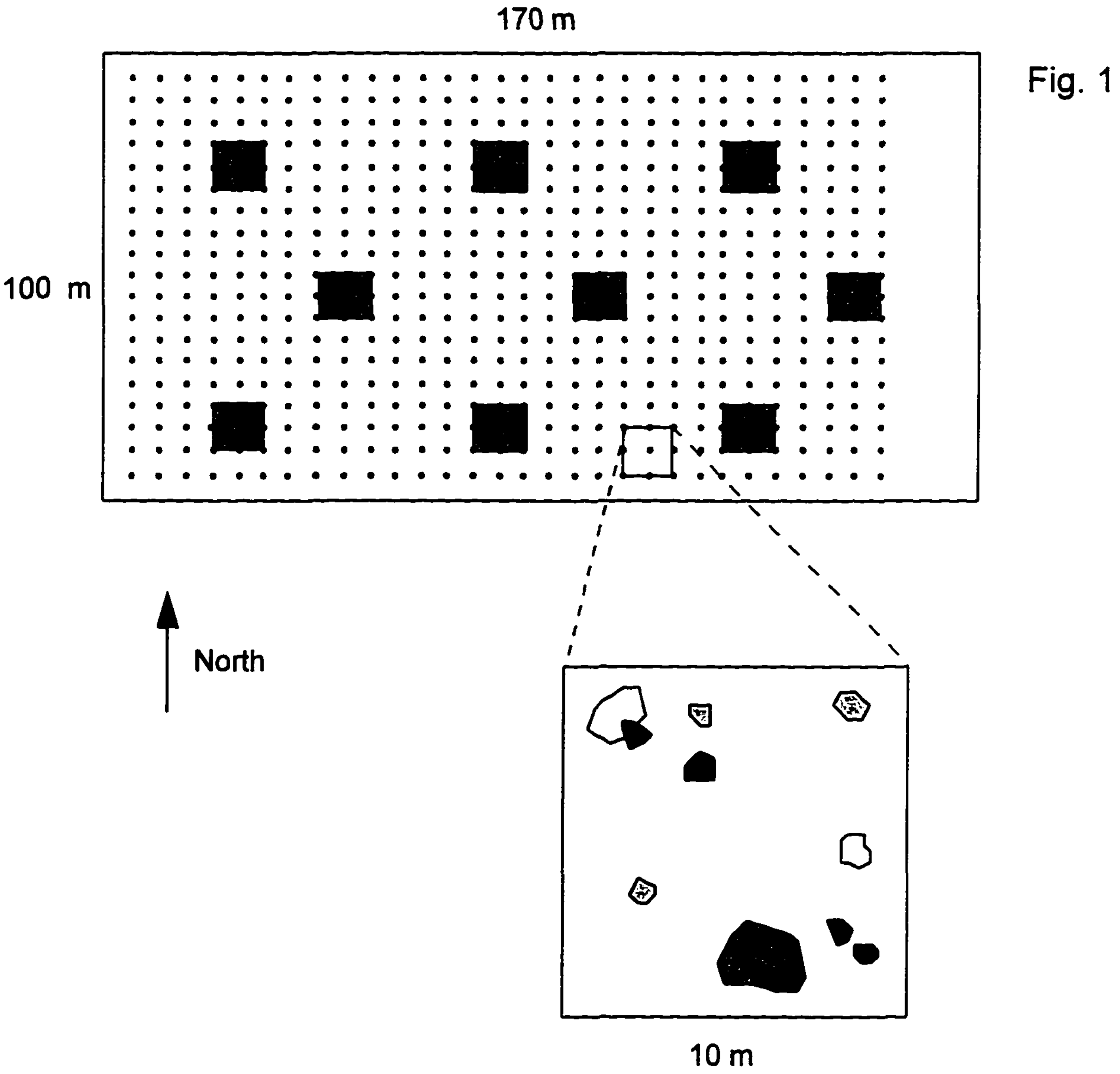
(I_M) calculated from the number of events in each 10 x 10 m grid square.

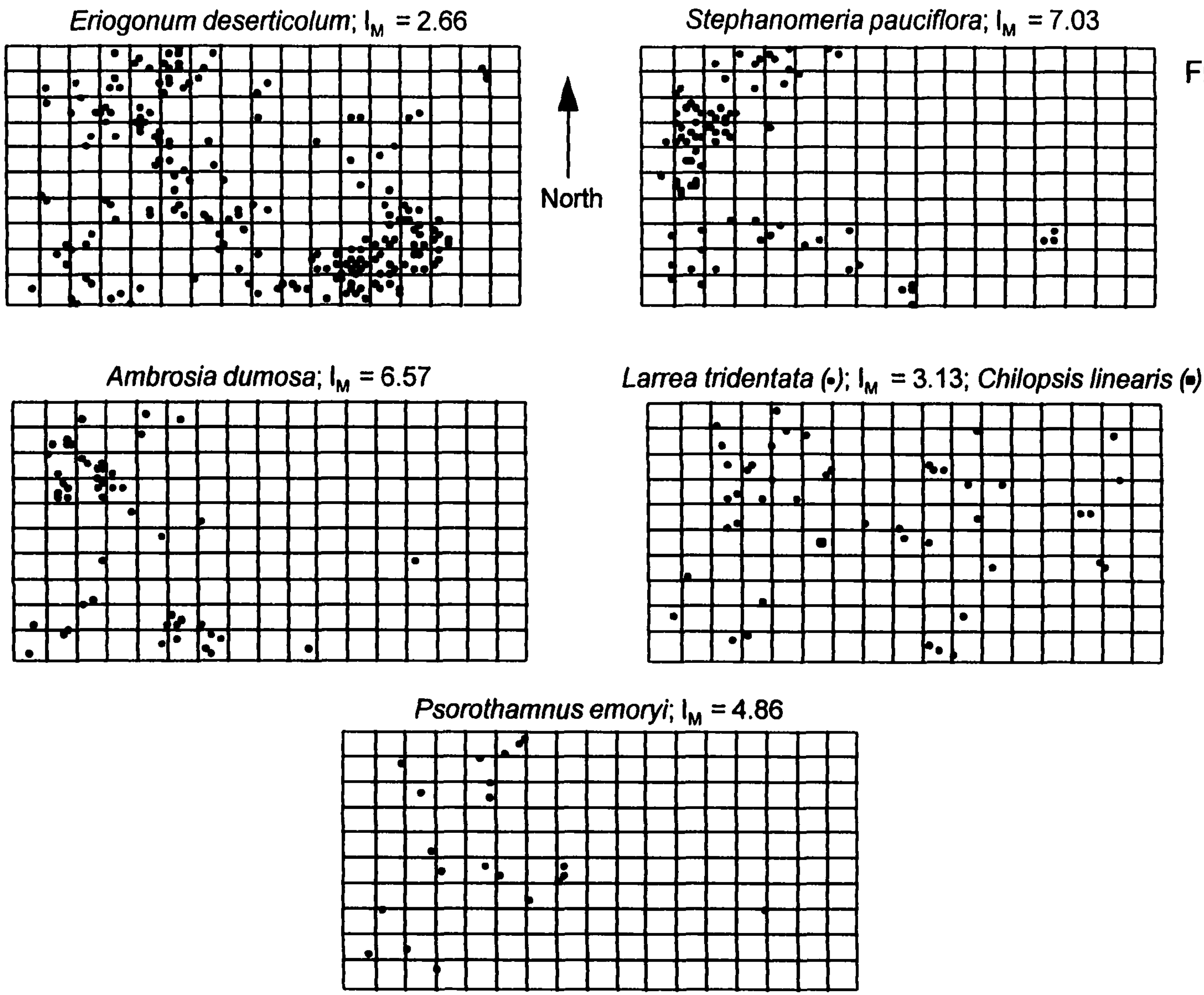
Figure 11. Mean number of females courted (+ SE) as a function of male home range center (HRC). "none" indicates a dispersed home range with no shrub as the center of activity. N refers to the number of males in each HRC category.

Figure 12. The sequence of courtship events and frequencies of outcomes for *D. dorsalis*. Width of lines are proportional to the number of observations. See text for descriptions of behaviors.

Figure 13. Regressions of log body length versus log head height, log head width between outer edges of supraocular scales (HW2), and log head height between upper edge of supraocular and jawline (HH2) for adult male and female *D. dorsalis*.

Figure 14. Residuals of the regressions of three head dimensions versus log body length, plotted as a function of log body length. Residuals were calculated from a regression on only those males for which status (dominant vs. low-rank) was known.


170 m
Fig. 1
100 m
North
10 m



Eriogonum deserticolum; I_M = 2.66

Stephanomeria pauciflora; I_M = 7.03

Ambrosia dumosa; I_M = 6.57

Larrea tridentata (•); I_M = 3.13; *Chilopsis linearis* (▪)

Psorothamnus emoryi; I_M = 4.86

Fig. 2

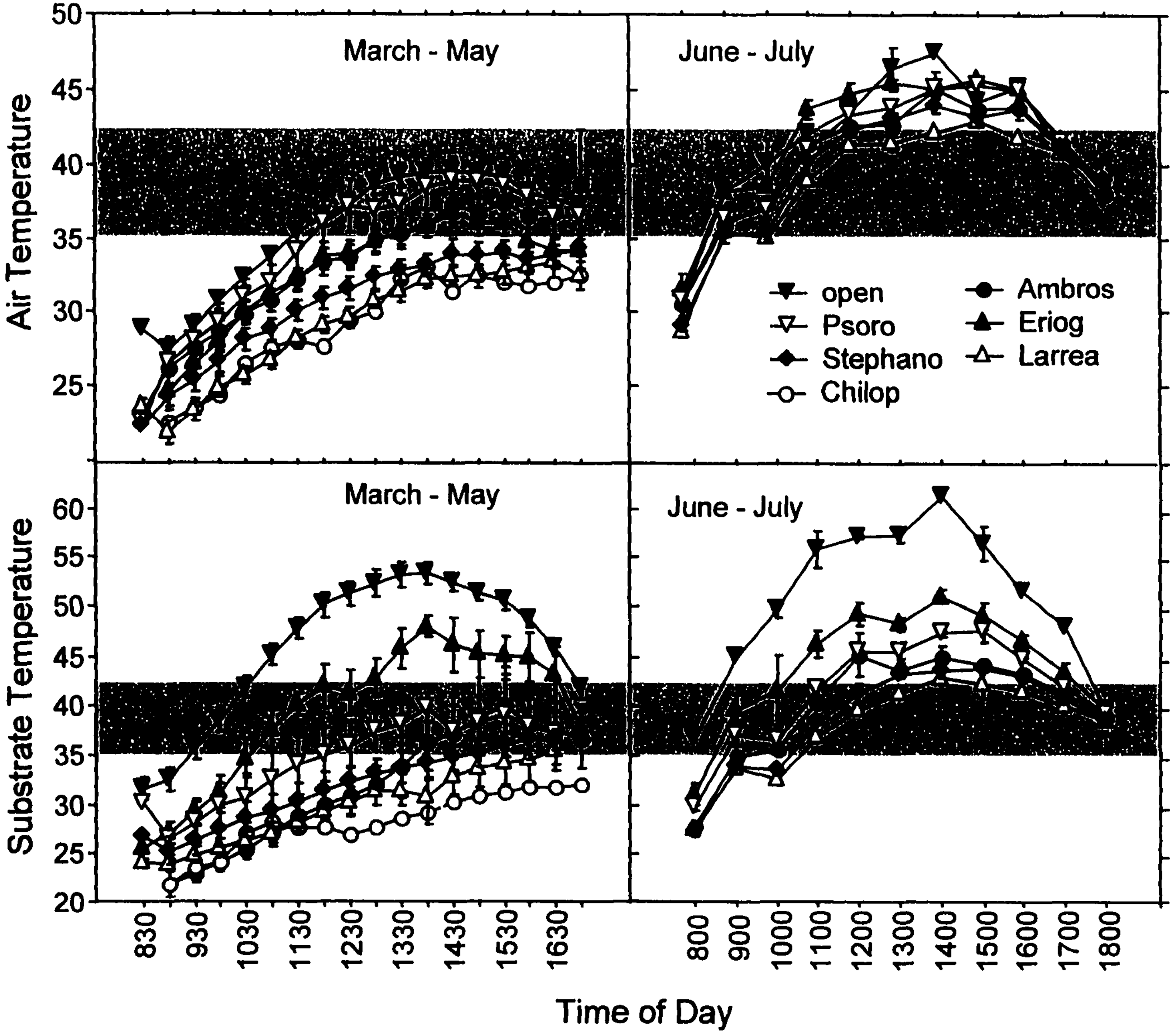

March - May
June - July
March - May
June - July
Air Temperature
Substrate Temperature
Time of Day
50
45
40
35
30
25
60
55
50
45
40
35
30
25
20
830
930
1030
1130
1230
1330
1430
1530
1630
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
▼ open
▽ Psoro
◆ Stephano
○ Chilop
● Ambros
▲ Eriog
△ Larrea

Fig. 3

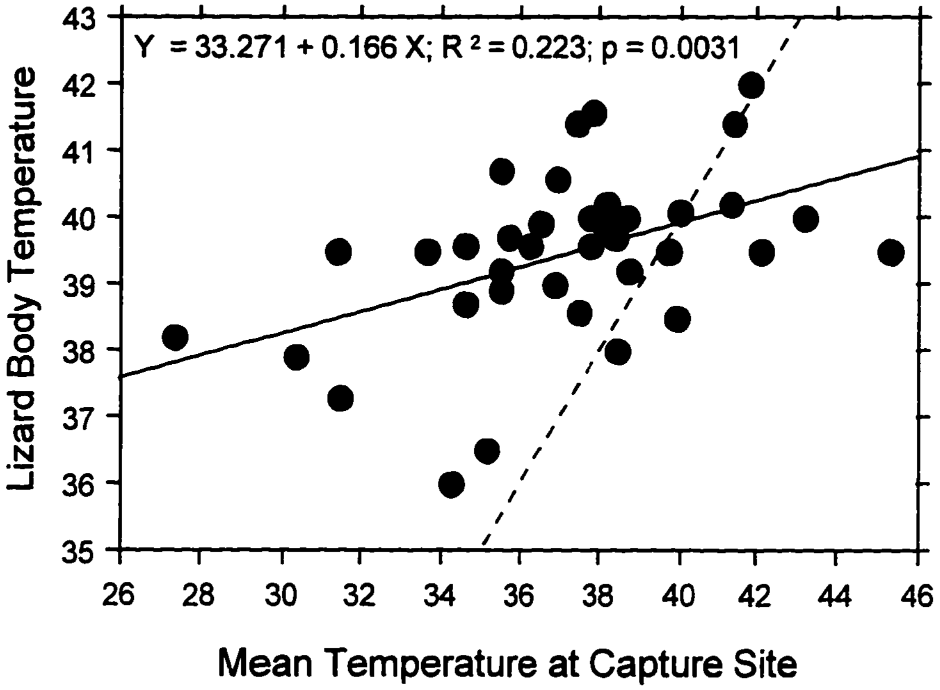

Y = 33.271 + 0.166 X; R 2 = 0.223; p = 0.0031
Lizard Body Temperature
Mean Temperature at Capture Site
43
42
41
40
39
38
37
36
35
26
28
30
32
34
36
38
40
42
44
46

Fig. 4

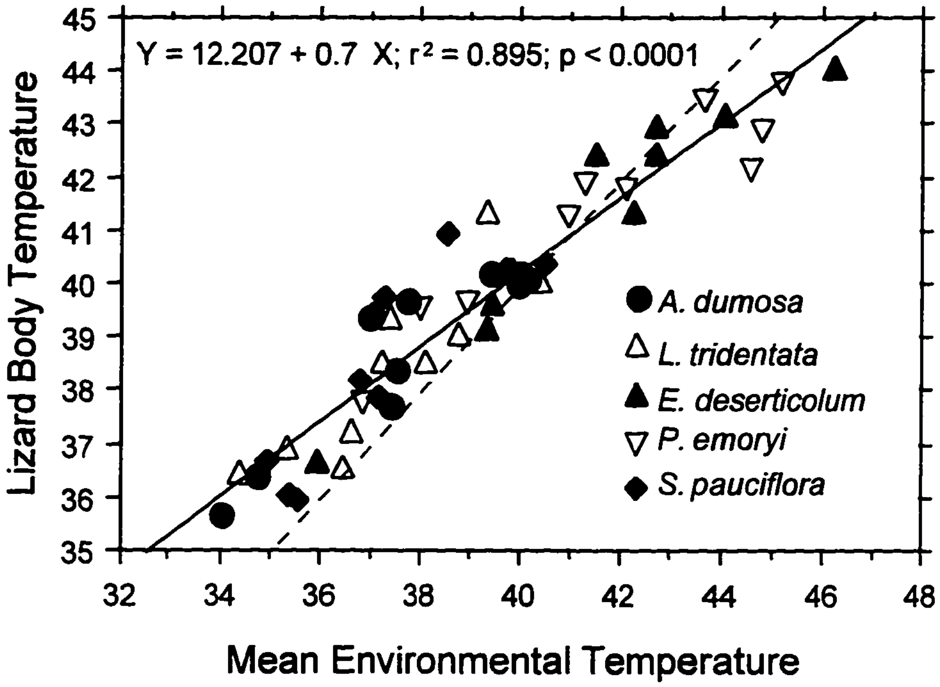

Y = 12.207 + 0.7 X; r² = 0.895; p < 0.0001
Lizard Body Temperature
Mean Environmental Temperature
45
44
43
42
41
40
39
38
37
36
35
32
34
36
38
40
42
44
46
48
● A. dumosa
△ L. tridentata
▲ E. deserticolum
▽ P. emoryi
◆ S. pauciflora

Fig. 5

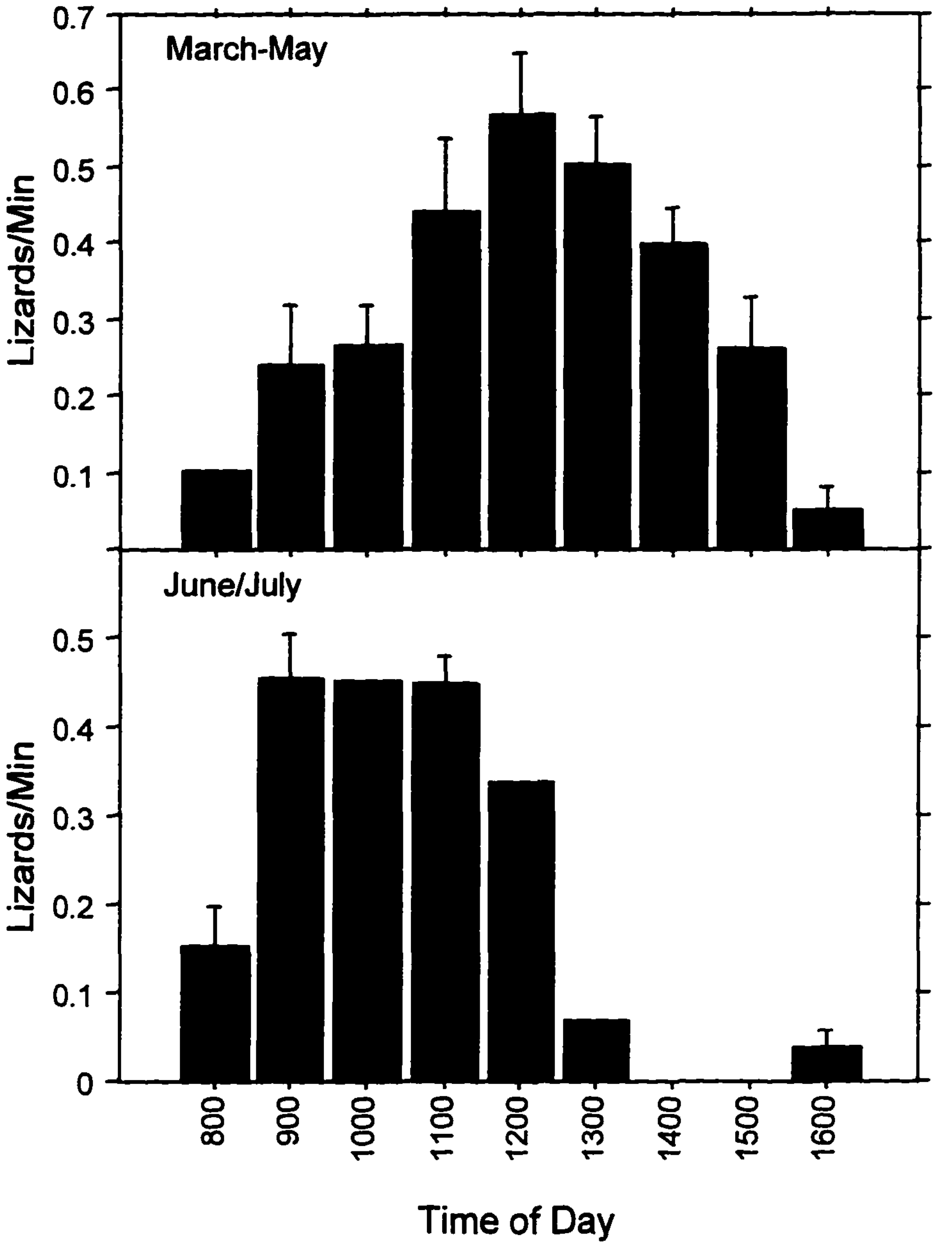
March-May
June/July
Lizards/Min
Lizards/Min
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.5
0.4
0.3
0.2
0.1
0
800
900
1000
1100
1200
1300
1400
1500
1600
Time of Day

Fig. 6

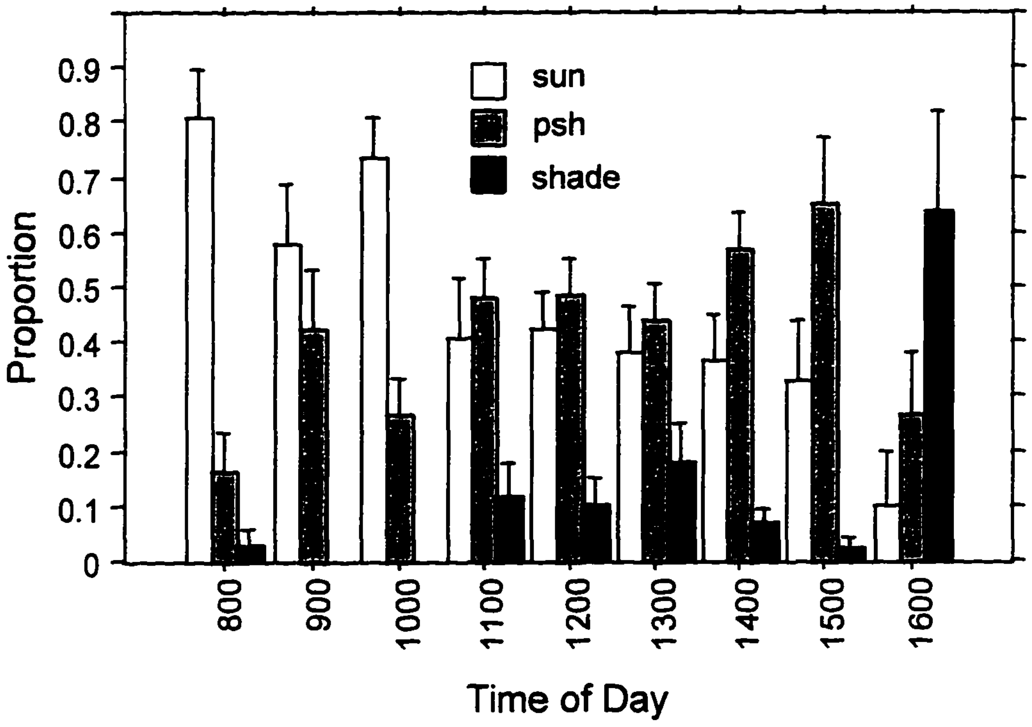
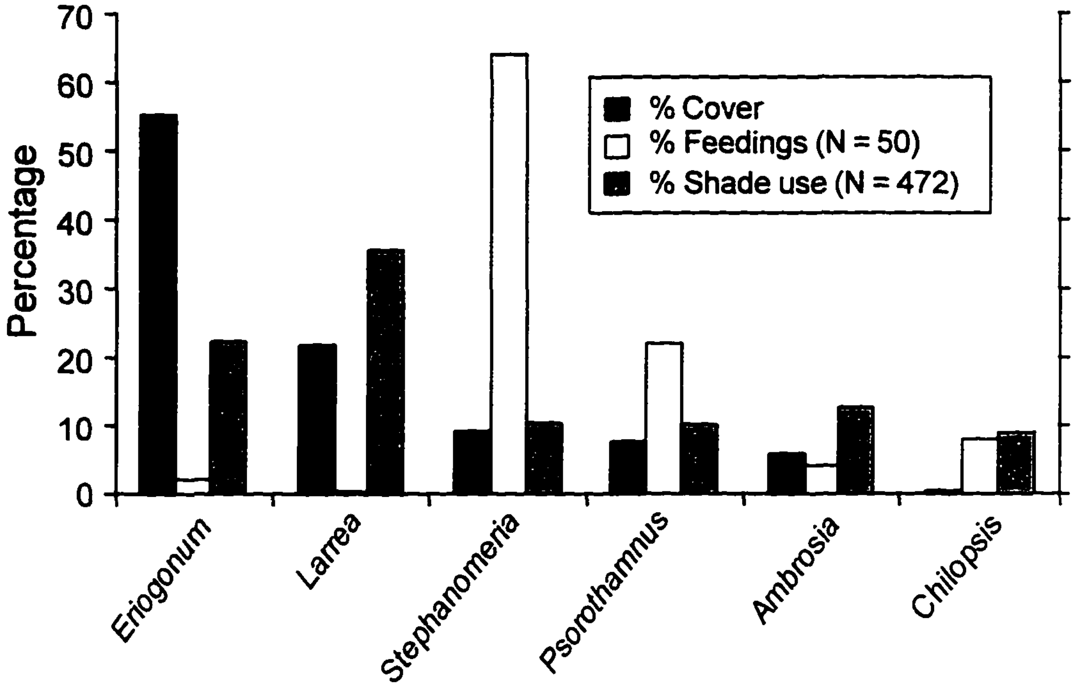

0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion
□ sun
▨ psh
■ shade
800
900
1000
1100
1200
1300
1400
1500
1600
Time of Day

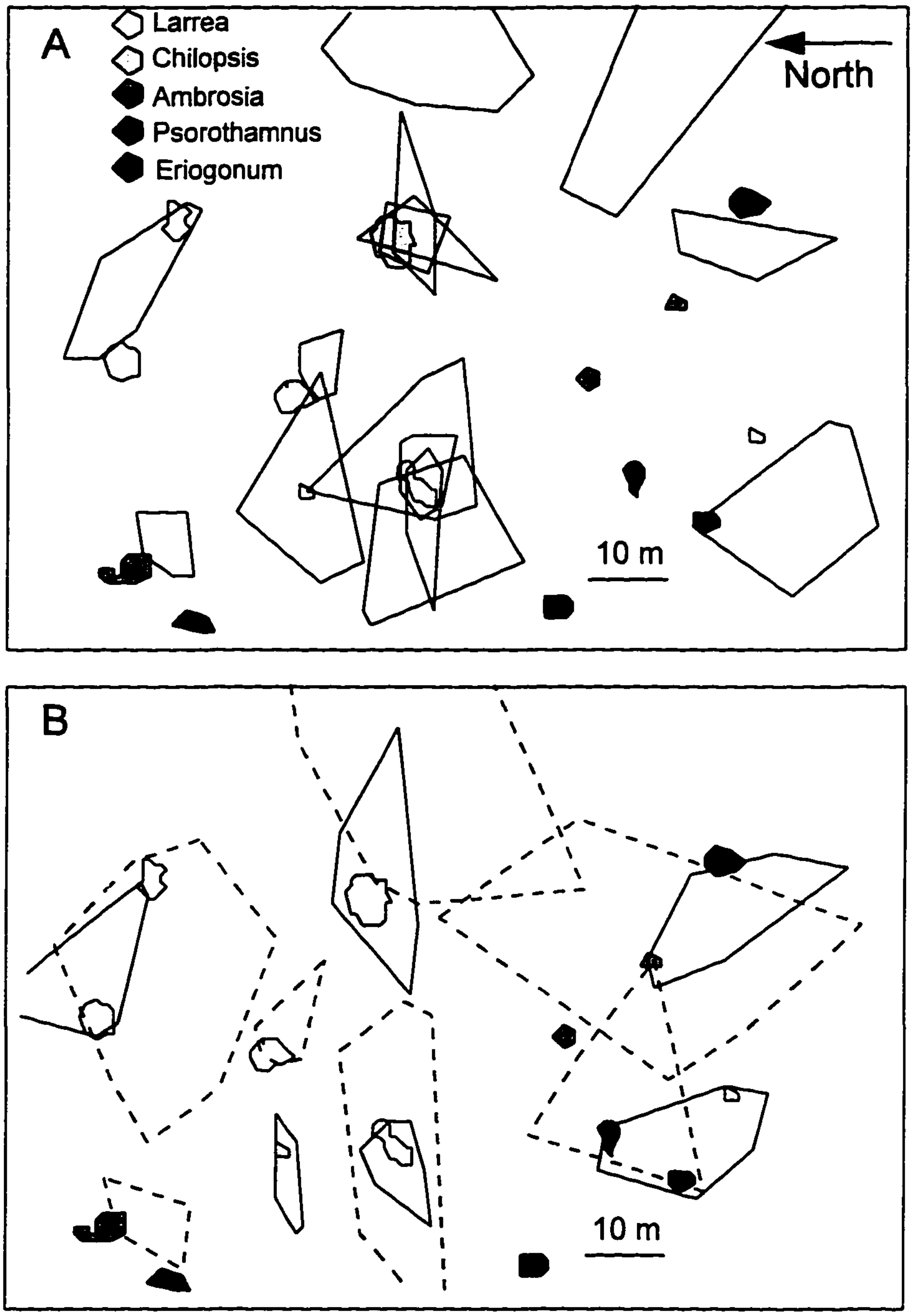
Fig. 7

Fig. 8



70
60
50
40
30
20
10
0
Percentage
% Cover
% Feedings (N = 50)
% Shade use (N = 472)
Eriogonum
Larrea
Stephanomeria
Psorothamnus
Ambrosia
Chilopsis

Fig. 9


A
Larrea
Chilopsis
Ambrosia
Psorothamnus
Eriogonum
North
10 m
B
10 m

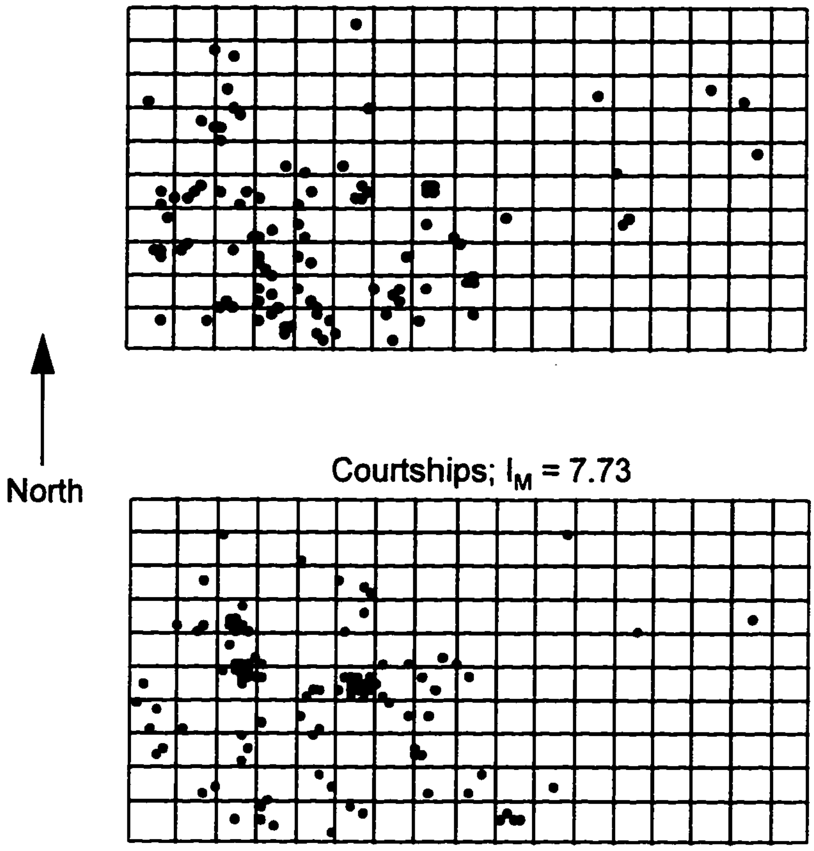


Fig. 10

Feedings; $I_M = 2.8$

Courtships; $I_M = 7.73$

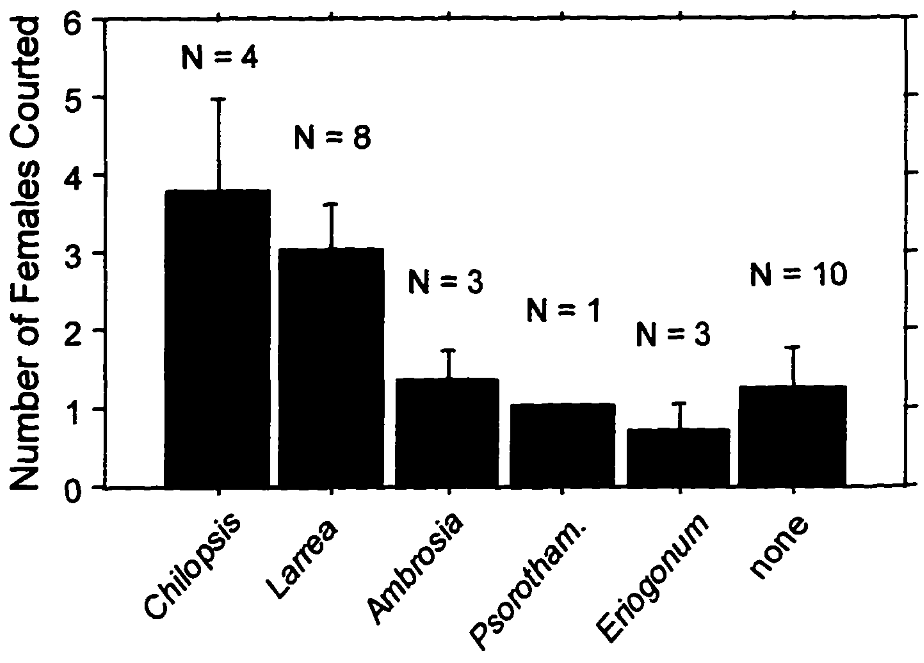
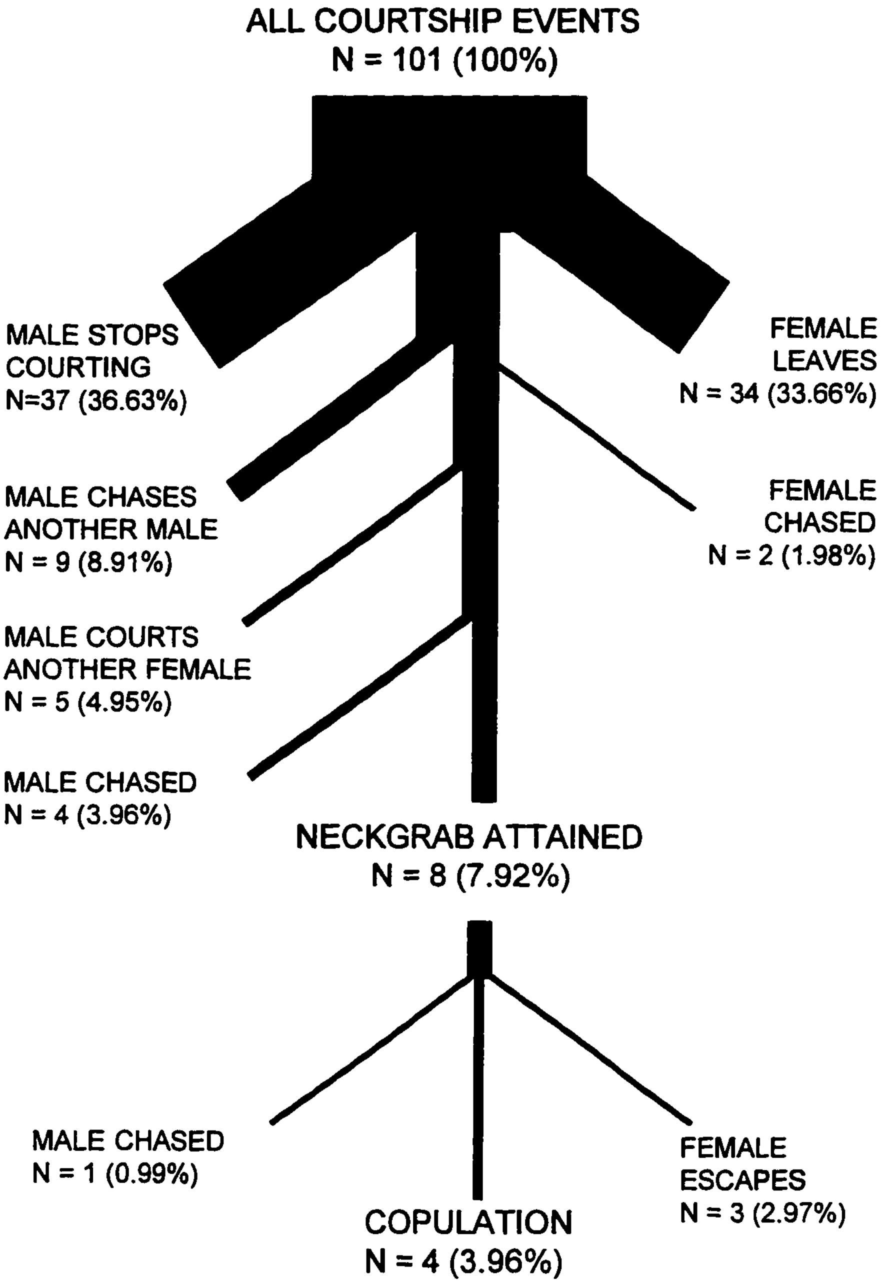

Number of Females Courted
0
1
2
3
4
5
6
N = 4
N = 8
N = 3
N = 1
N = 3
N = 10
Chilopsis
Larrea
Ambrosia
Psorotham.
Eriogonum
none

Fig. 11

Fig. 12


ALL COURTSHIP EVENTS
N = 101 (100%)
MALE STOPS COURTING
N=37 (36.63%)
FEMALE LEAVES
N = 34 (33.66%)
MALE CHASES ANOTHER MALE
N = 9 (8.91%)
FEMALE CHASED
N = 2 (1.98%)
MALE COURTS ANOTHER FEMALE
N = 5 (4.95%)
MALE CHASED
N = 4 (3.96%)
NECKGRAB ATTAINED
N = 8 (7.92%)
MALE CHASED
N = 1 (0.99%)
FEMALE ESCAPES
N = 3 (2.97%)
COPULATION
N = 4 (3.96%)

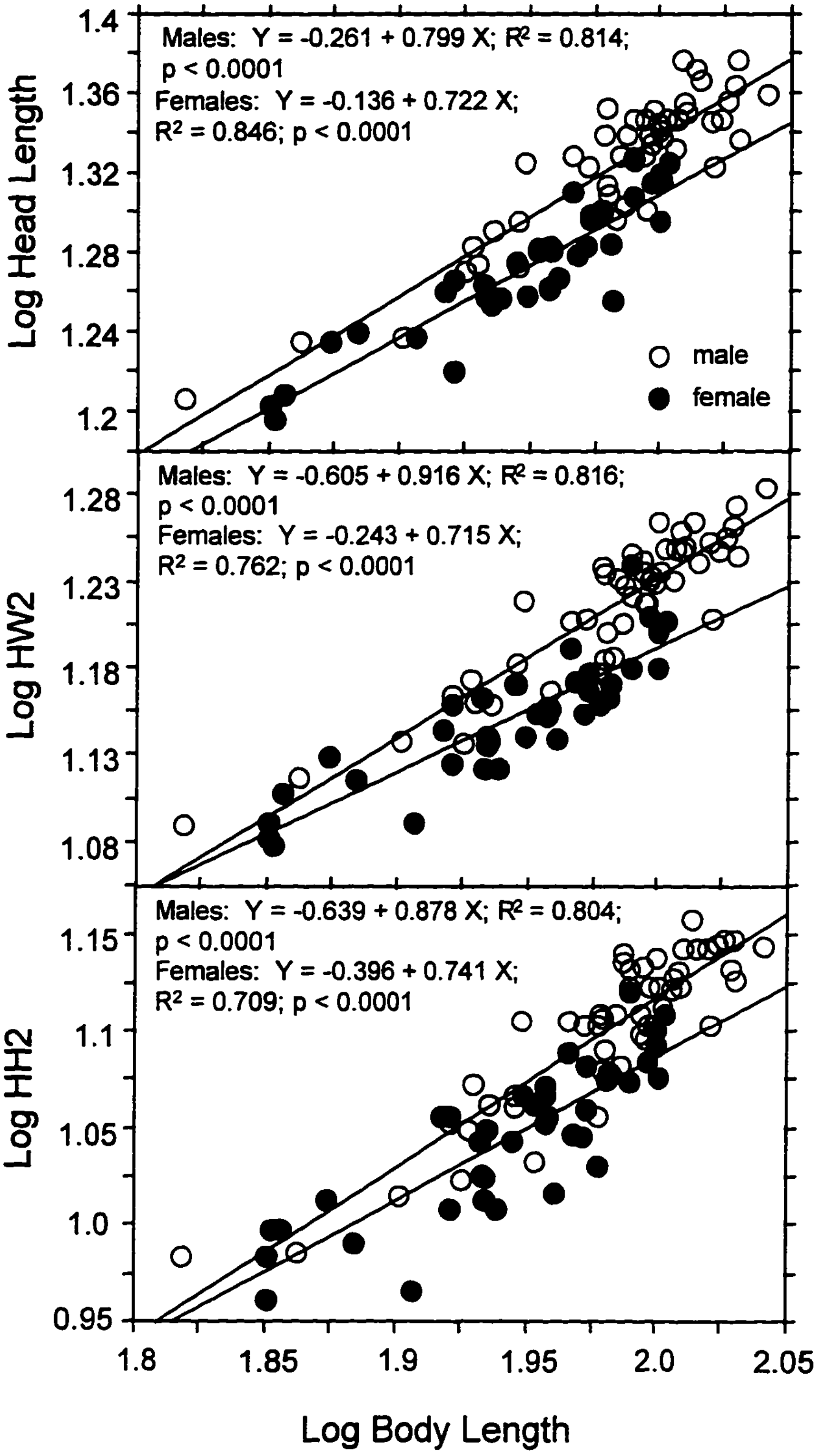

Males: Y = -0.261 + 0.799 X; R² = 0.814; p < 0.0001
Females: Y = -0.136 + 0.722 X; R² = 0.846; p < 0.0001
○ male
● female
Log Head Length
1.4
1.36
1.32
1.28
1.24
1.2
Males: Y = -0.605 + 0.916 X; R² = 0.816; p < 0.0001
Females: Y = -0.243 + 0.715 X; R² = 0.762; p < 0.0001
Log HW2
1.28
1.23
1.18
1.13
1.08
Males: Y = -0.639 + 0.878 X; R² = 0.804; p < 0.0001
Females: Y = -0.396 + 0.741 X; R² = 0.709; p < 0.0001
Log HH2
1.15
1.1
1.05
1.0
0.95
1.8
1.85
1.9
1.95
2.0
2.05
Log Body Length

Fig. 13

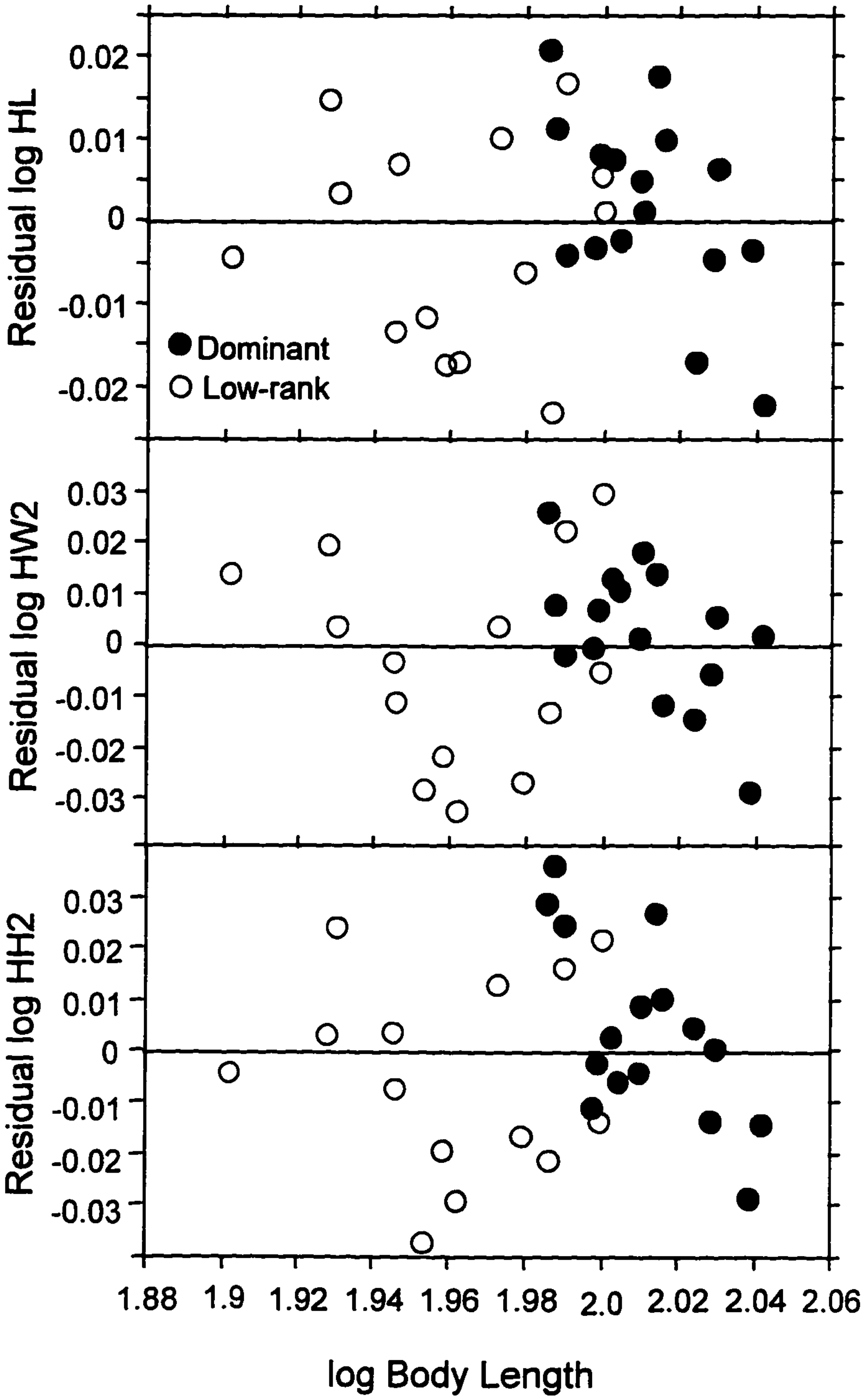

Residual log HL
0.02
0.01
0
-0.01
-0.02
● Dominant
○ Low-rank
Residual log HW2
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
Residual log HH2
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
1.88
1.9
1.92
1.94
1.96
1.98
2.0
2.02
2.04
2.06
log Body Length

Fig. 14

CHAPTER 3: MATING SYSTEMS AND SEXUAL DIMORPHISM IN THE IGUANIDAE: THE IMPORTANCE OF SHELTER

Abstract -- I analyzed the ecological factors impinging on the spatial distribution of individuals, and resultant influences on the mating systems, among species of the herbivorous lizard family Iguanidae. This group offered the opportunity to examine how large-scale resource distribution (the distribution of food and shelter from predators) can have impacts on local mate competition and subsequent patterns of sexual dimorphism. The ecological distribution of shelter was mapped onto alternative phylogenies of the family Iguanidae to examine the evolutionary correspondence between changes in the mating system and changes in the degree to which shelters were clumped in space. Examination of the literature revealed that iguanids are often dependent on very isolated shelters from predation, which has led to resource defense polygyny (RDP) in many species, with intense levels of mate competition among males. However, non-RDP systems have evolved independently in three lineages, and all of these transitions occur in taxa in which shelter has become less limiting. I next mapped the degree of sexual dimorphism onto the same phylogenies to examine the correspondence between mating system and the nature of sexual dimorphism. Sexual dimorphism does not correspond closely either with mating systems or with degree of clumping of shelter. Further, contrast analyses on dimorphisms in head size reveal that different aspects of head dimorphism (head length vs. head circumference) can evolve independently, with a very weak correlation between them.

INTRODUCTION

Questions concerning the evolution of animal mating systems are inherently complex, since such systems are the product of a variety of ecological, behavioral, and morphological components, all of which may be constrained by phylogeny (Emlen and Oring 1977; Bradbury 1985; Davies 1991; Clutton-Brock et al. 1992). Variation in male mating behavior is related to the degree of paternal care in the rearing of young and to the defensibility of females (Orians 1969; Trivers 1972). In systems in which males contribute no parental care, the degree to which females can be monopolized becomes crucial. Female aggregation around clumped resources, for instance, may set the stage for a high degree of polygyny (i.e., a high environmental potential for polygamy, EPP, sensu Emlen and Oring 1977).

Determining which factors limit animal home ranges and therefore contribute most significantly to the evolution of social systems is a difficult task because it involves quantifying resource values and distributions for a potentially large number of resources on which an animal depends. However, studies on a variety of taxa showed that food (Ims 1987; Davies et al. 1995), shelters or resting sites (Baird and Liley 1989; Baldi et al. 1996), nesting or oviposition sites (Howard 1978; Alcock 1987), and thermal patches (Pleszczynska 1978; Carey 1991) play crucial roles in determining the nature of habitat use and the opportunity for polygamy.

No broad generalizations have yet emerged concerning taxonomic predilection for dependence on a certain type of resource, although among endotherms, individuals often aggregate around food supplies, which are inevitably patchy at some scale (e.g., Ims

1987). In fact, some models of territory and home range quality assume the preeminent importance of energetic gains of home range placement (e.g., Hixon 1987). For ectotherms, however, other factors may often equal or exceed the influence of food patchiness in determining individual spacing patterns, because their metabolism is less dependent on constant sources of food. Individual space use by lizards may be determined by thermal patches (Waldschmidt and Tracy 1983; Christian et al. 1983; Christian and Tracy 1985; Gier 1997), availability of basking sites or predator retreats (Gil et al. 1990), food patches (Simon 1975; Hews 1993), or social factors (Stamps 1988). Among many iguanian lizards, investigations into relative resource importance are simplified due to small home ranges of females, whose philopatry often reveals the resource most restricting their movements (see reviews in Rose 1982; Stamps 1983). Female philopatry in turn promotes male mate monopolization and the evolution of resource-defense polygyny, the most common mating system among iguanians (Stamps 1983). Theoretically, one would expect the resource most responsible for mating system evolution to be the most narrowly distributed of the subset of crucial resources, not necessarily the one most closely tied to growth, survival, or reproduction.

The lizard family Iguanidae (sensu Frost and Etheridge 1989) includes eight genera of herbivorous, medium- to large-bodied species, distributed thoughout the northern Neotropics and Galapagos Islands but extending north into the deserts of the southwestern United States and with an isolated genus in Fiji (de Queiroz 1987). For a family of such low diversity and ecological uniformity (most large, all sedentary and herbivorous, residing in tropical or other hot climates), the iguanids exhibit a great range of mating systems, including leks, which are not known in any other reptiles. This diversity of mating systems may be due at least in part to several ecological factors that distinguish iguanids from insectivorous lizards. First, as generalist herbivores, many iguanids are less limited by food than most insectivores; exceptions may include species inhabiting highly seasonal, xeric habitats. Also, the relatively large body size of most iguanids complicates the matter of predator escape in ways not typical of most insectivores, for whom adequate refuge is widely available in any structurally complex habitat. Although large body size reduces the potential pool of predators, it leads to difficulties in escaping large predators, since large iguanids must rely on large shelters such as permanent burrows or crevices. Such shelters are typically limited in distribution, and may form the focal points of adult home ranges. Thus, for those iguanids living in predator-rich environments, and in the absence of food limitations, the distribution of retreats may serve as a key resource in structuring mating systems.

Another evolutionary byproduct of the social system is the degree of sexual dimorphism. Lizards have served as model systems to examine the morphological manifestations of intensely competetive mating systems. If ecological factors influence the degree of local mate competition, sexual dimorphism should reflect this, and species with more competetive mating systems should have stronger sexual dimorphism. In lizards, these selective pressures are often manifested in differences in head allometry between males and females, since male-male combat is a salient feature of lizard mating systems and the head is the primary weapon used in contests (Carothers 1984; Vitt and Cooper 1985; Hews 1990).

Investigating ecological factors (e.g., shelter distribution) and their putative evolutionary effects (sexual dimorphism) requires factoring out the influence of phylogeny, since patterns of behavior may reflect evolutionary history rather than present ecology (Brooks and McLennan 1991). In this paper, I use phylogenies as a tool to examine the hypothesis that the distribution of permanent retreats has influenced the evolution of mating systems and sexual dimorphism in iguanids. Specifically, I predict that 1) resource-defense mating systems will evolve in lineages that rely on predator refuges that are highly clumped in space, such as widely scattered rock outcrops; and 2) departures from resource defense polygyny will occur in lineages that do not rely on clumped shelters from predators; and 3) the strongest sexual dimorphism will occur in species with the most competetive mating systems.

METHODS

Mating System Designations

I used published sources to characterize the mating systems of iguanids. Such sources rarely designate explicit categories of mating systems; thus, I have interpreted their descriptions and placed species into one of three categories. First, resource defense polygyny (RDP) is defined as male territoriality based on resources around which females aggregate (Davies 1991). RDP includes instances in which more than one male is associated with a group of females gathered aound an isolated resource, if one male is behaviorally dominant and at least partially excludes other males from access to the females. Also, RDP includes examples of serial or sequential polygyny if the females utilize resources in the male's territory during an extended courtship. The second mating system category is stable monogamy/polygynandry (Mono), an ad hoc category created to describe the social system of insular giant chuckwallas (Sauromalus hispidus and S. varius; see Results). In these species, one or more males form more or less permanent associations with a variable number of females. Monogamous, polygynous, and polygynandrous groups may occur within the same population, although monogamy and bigamy are most common. Although these systems are variable and not entirely understood, they are distinguishable from RDP based on a relative lack of male-male aggression and site exclusion. The third mating system category is leks, which are arena-based systems in which females choose from a number of displaying or courting males. A central characteristic of lek mating systems is clustered male territories that are not resource-based (Emlen and Oring 1977; Bradbury 1981, 1985). This is often difficult to demonstrate for lizards since male territories may contain thermal patches that serve as resources but require special methods to quantify (e.g., Waldschmidt and Tracy 1983; Christian and Tracy 1985; Adolph 1990).

For all cases of RDP, I denoted whether the direct object of male territoriality is burrows or food, since most ecobehavioral studies focused on the relationships of animals to these two resources.

I have not characterized the mating system of a number of species that are poorly studied or defy clear categorization. Few members of the genera Ctenosaura and Cyclura have been studied sufficiently to characterize their social systems, and I only treated those species for which behavioral data are available. Similarly, a full description of the social systems of the two species of Fijian iguanas (Brachylophus) is unavailable, although preliminary work (Gibbons and Watkins 1982) suggests a system convergent with I. iguana.

Predator Refuge Dispersion

I characterized the degree to which retreats from predators are dispersed in space. For most species, retreats are burrows dug in soil, holes in hollow trees, or rock crevices. Distances between groups of shelters are rarely quantified in the literature; however, it is generally possible to place shelter dispersion into the broad categories of clumped, dispersed, and intermediate. The category clumped was used if a number of females (generally more than five) use a group of burrows (or crevices, etc.) that are located in an isolated habitat that is separated from other such habitats by a distance exceeding three times the diameter of a female's normal home range. Isolated rock outcrops and large hollow trees with multiple entrance holes are examples of habitats used by iguanids that meet this requirement. Dispersed shelters implies that female home range overlap is minimal, with nearly all females having separate burrow entrances or burrow systems. Intermediate clumping implies local areas of overlap of no more than three to four females in habitats of otherwise uniform female distribution.

Phylogenetic Reconstruction

Phylogenetic hypotheses (cladograms) for the relationships of the Iguanidae follow Sites et al. (1996), and are based on consensus trees derived from combining de Queiroz' (1987) and Norell and de Queiroz' (1991) morphometric-based trees with mitochondrial DNA data. I mapped qualitative shelter distribution and mating systems onto the independently derived phylogenies to examine the evolutionary correspondence between these two variables.

One of the assumptions made when using phylogenies to test the evolution of traits is that the characters used to construct the phylogeny are independent of the traits being mapped onto it. Mapping patterns of sexual dimorphism in head dimensions violates this assumption to some degree, because skull morphology played a major role in shaping the topology of the morphology-based cladograms (over 30 of the 95 characters used were skull features; de Queiroz 1987; Norell and de Queiroz 1991). The importance of skull features is diminished somewhat in the consensus trees used here (Sites et al. 1996) due to the inclusion of molecular data. This possible nonindependence would affect the present study if the nature of the skull of a particular genus made that genus more likely to develop sexual dimorphism. This seems unlikely, since characters that vary between the sexes would be less likely to be of use in phylogenetic construction. Since I am comparing head morphologies between the sexes within species, rather than between species, I am assuming that the evolution of sexual dimorphism is independent of the skull characters used in part to build the trees.

Morphological Data

I used data from Carothers (1984) on measurements of dimorphism in head length (HL) and head circumference (HC) to quantify sexual dimorphism for nine species from five genera of iguanids. Male-female dimorphism is quantified as the intersexual difference in slopes of the regression between log transformed snout-vent length (SVL) and head dimension. When the differences in slope are statistically significant (ANCOVA with SVL as covariate; Carothers 1984), then males and females differ in the nature of the head-body growth allometry. Although this measure does not detect sexual size dimorphism in the absence of allometric differences, it is appropriate for the present analyses since the nature of male-male combat among lizards tends to result in different head-body proportions between males and females (e.g., Vitt and Cooper 1985; Hews 1990). To quantify dimorphism in body size, I used Carothers' data on the ratio of male to female SVL (male-female ratio, MFR) as an index of length dimorphism. This measure is not completely independent of the head measurements, since HL forms part of SVL. Thus, using this measure to investigate the evolution of head dimorphism (by regressing dimorphism in HL against MFR, for instance) will potentially mask extremes in body size dimorphism that would be more apparent if body length (head not included) is used instead of SVL.

To examine the evolutionary history of sexual dimorphism in this group, I calculated independent contrasts (Felsenstein 1985) between taxa for dimorphisms in HL and HC and for MFR. Since these values are quantifications of sexual dimorphism and not standard morphological measurements per se, the resultant comparisons reconstruct evolutionary changes in the nature of dimorphism. By regressing contrasts in HL with those in HC, I can determine the extent to which dimorphisms in these two characters coevolve, to examine the possibility of differing evolutionary forces acting independently on these two head measurements. Secondly, by regressing contrasts in the two types of head dimorphism against contrasts in MFR, I will examine whether changes in body size are accompanied by predictable changes in head shape.

Although the phylogenetic contrast method has the advantage of deriving normally distributed data from phylogenies, it assumes that the complete phylogeny, including branch lengths, is known (Felsenstein 1985). The present phylogeny is partial (several species are excluded) and branch lengths are unknown; however, branch lengths can be estimated with various techniques. I used a simple and arbitrary rule of assigning a value of one to terminal branches, and progressively larger values (in increments of one) as relationships become more distant (Martins 1994). In the case of the unresolved polytomy for the genus Sauromalus, I calculated contrasts for all three possible relationships among these three species (assuming a dichotomous branching pattern) and performed the analyses for each. All regressions on contrast data were forced through the origin by adding or subtracting the intercept value to each data point from an initial regression.

RESULTS

Mating systems and resources

Most iguanids for which data are available engage in resource-defense polygyny (table 1), with burrows or other retreats usually being the direct object of male territoriality. Food sources have been identified as the predominant defended resource only for C. carinata (Iverson 1979), and even in this case food was followed closely in importance by the burrows present in male territories. Although food sources play a role in the social systems of some iguanids (e.g., S. obesus, Berry 1974; C. subcristatus, Werner 1982; C. similis, Gier 1997), it is more typical for feeding areas to function as zones of lowered aggression, where individuals tolerate close proximity of would-be sexual competitors (e.g., Cowles 1946; Evans 1951; Johnson 1965; Carothers 1981; Case

1982). I have not designated either burrows or food as the crucial resource for D. dorsalis, because neither resource is under more consistent control by males, and both resources may be less important than optimal thermal patches (Gier 1997).

Although included in the RDP category, the Galapagos land iguana Conolophus pallidus is serially or sequentially polygynous. Females seasonally leave their normal home ranges to travel to remote nesting sites to lay eggs; along the way they pass through male territories, where they copulate before continuing to the nesting areas (Christian and Tracy 1982). The male territories differ from the leks of other species (see below) in that females reside with the male for a number of days before continuing, during which time they use the burrows in the male's territory, similar to other RDP systems. The insular Cyclura carinata also exhibits serial polygyny, with females relying on food and burrows within male territories (Iverson 1979), although the length of female residency has not been reported. Female-defense polygyny or harem polygyny, in which the females themselves are defended (e.g., Hogg 1984; Webster 1994) has not been demonstrated for any iguanid.

The insular giant chuckwallas, Sauromalus varius and S. hispidus exhibit monogamy/polygynandry (Mono); in these species population densities are low and males and females form more or less permanent associations with variable numbers of the opposite sex (Case 1982, 1983; Smits 1985). There is little male-male aggression (even when males are experimentally transferred to another's home range; Case 1982), which is a salient feature of all other polygynous iguanids. Also, male home ranges overlap extensively (Smits 1985), a condition atypical of RDP.

Two species are characterized as having leks. Males of the Galapagos marine iguana, Amblyrhynchus cristatus (Carpenter 1966; Boersma 1983; Wikelski et al. 1996), and the common iguana, Iguana iguana (Dugan 1982; Rodda 1992), defend small clustered territories that apparently function solely for mating. Females of both species often visit a number of these territories before copulating with a male. The designation of A. cristatus as a lekking species may seem to contradict the results of Trillmich (1983) and Rauch (1985), who showed that at high population densities, females are attracted to the thermal properties of the territories of some males (i.e., RDP). However, Rauch (1985) showed that male territory placement is not closely tied to female basking sites; a study on a less dense population (Wikelski et al. 1996) showed that male territories functioned solely in reproduction. Iguana iguana and A. cristatus mating systems are also characterized by high levels of female harrassment by low-rank males in areas away from the main mating territories, another feature that has been theorized to play a role in the evolution of leks (Clutton-Brock et al. 1992; Stillman et al. 1993).

Predator Refuge Dispersion

Predator refuges exhibit a high degree of clumping in many species. Isolated rock outcrops with deep crevices are required by Ctenosaura and by S. obesus; these habitats result in localized populations of individuals widely separated from other populations (Evans 1951; Berry 1974; Carothers 1981; Gier 1997). Some Ctenosaura also use hollow trees (Duellman and Duellman 1959; Gier 1997), which are similarly limiting in distribution. The genera Conolophus and Cyclura dig burrows in soil, and exhibit more variability in the degree to which these retreats are clumped (Christian and Tracy 1982;

Dugan and Wiewandt 1982; Werner 1982).

In contrast, retreats are relatively widespread for some iguanids, including the two insular Sauromalus species (table 1), which live in shallow crevices and small caves in their arroyo habitats (Case 1982; Smits 1985). I also include A. cristatus in this category because retreat is available in lava fissures and in widely available crevices rather than burrows (Rauch 1985; note, however, that the most important predators of A. cristatus are aquatic; Carpenter 1966; Boersma 1983). Refuges are also not limiting for I. iguana, which does not rely on discrete refuges per se, but which escapes into trees (from terrestrial predators) or by diving out of the trees into water (from arboreal/aerial predators) (Dugan 1982; Rodda 1992).

Dipsosaurus dorsalis has an intermediate level of predator retreat clumping. In this species, burrows, which often are located at the base of large shrubs, serve as retreats, and in some populations, some burrows are aggregated around large shrubs (e.g., Alberts 1993). However, there is a great deal of variation in the degree to which shrubs and burrows are clumped over the range of this species, with very low female home range overlap demonstrated for some populations (Krekorian 1976). Other populations (e.g., Gier 1997) exhibit intermediate levels of burrow clumping at the bases of shrubs, with other burrows more regularly scattered over barren ground.

Phylogenetic Reconstruction

The first tree (Fig. 1A) was constructed from a data matrix excluding characters with two or more homoplasies; the second tree (Fig. 1B) only used consistent characters. Although at the species level tree 1B has a higher consistency index than tree 1A (CI =

0.652 vs. 0.591), Sites et al. (1996) considered tree 1A the best-supported hypothesis at the genus level. For this reason, contrast analyses (see below) are based on tree 1A. However, tree 1B, while less robust at this level, cannot be rejected. I have excluded the genus *Brachylophus*, since no data on mating behavior is available for the genus (*Brachylophus* is hypothesized to represent the basal taxon and thus a sister group to all other iguanids). I have relied on published phylogenies only to the genus level, and have added species here without resolving any relationships, thus creating the polytomies for the genera *Sauromalus* and *Ctenosaura*. No unambiguous outgroup is available for the family Iguanidae since it is part of an unresolved polytomy of several lizard families which collectively forms a sister taxon to all other lizards (Frost and Etheridge 1989). Sites et al. (1996) alternately used Phrynosomatidae, Hoplocercidae, and Opluridae to root their consensus trees, but the families Chameleonidae, Corytophanidae, Crotaphytidae, Polychrotidae, and Tropiduridae are all equally plausible outgroups.

RDP is assumed to be the ancestral mating system because RDP is the most widespread mating system among iguanian insectivorous lizards (Stamps 1983), the group most phylogenetically related to iguanids (Frost and Etheridge 1989). The evolution of leks in *A. cristatus* and *I. iguana* occur on nonadjacent branches.

Intermediate shelter clumping was designated as ancestral for two reasons: it is. 1) the condition in *D. dorsalis*, the most basal taxon in this tree (but note the exclusion of *Brachylophus*, for whom refuge dispersion is unknown), and 2) the condition most typical of insectivorous iguanians (Stamps 1983), among which the iguanids arose (Frost and Etheridge 1989). I have denoted the evolution of dispersed predator refuges in

Iguana iguana and the insular Sauromalus species as occurring independently, although they occupy adjacent branches on fig. 1A and fig. 2. This decision was made because the dispersion of retreats for these ecologically distinct forms is due to very different environments (I. iguana is arboreal in forests; insular Sauromalus occur on xeric rocky islands). The two alternative hypotheses of relationships among the iguanids reveal four transitions from clumped to relatively more evenly distributed refuges; three of these are accompanied by a departure from the ancestral RDP mating system.

Sexual Dimorphism

Among the species for which quantitative data on sexual dimorphism are available, three of the four species exhibiting low to moderate degrees of predator refuge clumping also show lesser degrees of head dimorphism (fig. 2). Iguana iguana is the only such species showing dimorphism in both head length and circumference. Conversely, Conolophus subcristatus exhibits clumped refuges but is only dimorphic in head circumference (note, however, that the categorization of refuge clumping for this species is equivocal; table 1). There are only two evolutionary transitions to dispersed shelters on either tree 2A or 2B.

In general, there is no clear correspondence between mating system and the nature of head dimorphism when the dimorphism data are grouped into presence-absence categories. Head dimorphism seems to be independent of whether mating system is RDP, Mono, or lek (fig 2).

In calculating contrasts, results for these three permutations of the Sauromalus polytomy did not differ qualitatively, and I arbitrarily present the results of the branching pattern [S. obesus [S. varius + S. hispidus]]. Similarly, I calculated contrasts for both phylogenies (figures 2A and 2B), but only present data for those from fig. 2A because of its greater robustness at the genus level. Qualitative results were similar for fig. 2B.

Figure 3 reveals a significant positive association between evolutionary change in HL dimorphism and simultaneous change in HC dimorphism. However, there is a large amount of scatter in the data ($r^2 = 0.508$). Also, changes in the evolution of SVL dimorphism are poor predictors of simultaneous changes in head dimorphisms (fig. 4). There is no significant relationship between changes in MFR and changes in either of the head dimorphisms.

DISCUSSION

Mating systems and shelter

The ecological and physiological consequences of large body size in herbivorous lizards have been discussed (e.g., Pough 1973; Zimmerman and Tracy 1989), but social consequences have received less attention. Here, I have attempted to show that social evolution in the Iguanidae is influenced in part by the importance of avoiding predation. This is manifested, at least on mainland forms, by a strong reliance on large shelters, which tend to be highly localized within the habitats occupied by these animals.

Most iguanids exhibit resource defense polygyny, with burrows being the direct object of territory defense in most species (table 1). The defense of burrows by males is a tenable strategy in these species due in part to the extreme philopatry of females. Studies on female movements, especially those of mainland, burrow-dwelling forms (e.g., Evans 1951; Berry 1974; Krekorian 1976; Carothers 1981; Gier 1997) have consistently shown limited female movements centered around burrow openings. Most species studied also show specific burrow requirements. For instance, members of the genus *Ctenosaura* inhabit isolated rockpiles or hollow trees (Evans 1951; Duellman and Duellman 1959; Carothers 1981; Gier 1997) and *Sauromalus obesus* uses rock outcrops with deep crevices (Johnson 1965; Berry 1974). Members of the genera *Conolophus* and *Cyclura* dig permanent burrows (Iverson 1979; Dugan and Wiewandt 1982; Werner 1982); however, the extent to which burrow distribution is limited by friable soil is unknown for most species. As a general rule, RDP in many iguanids seems to have arisen as a result of a distribution of shelter that led to a localized dispersion of females.

Although the distribution of shelter may play a role in space use for many insectivorous lizards, burrow defense appears to be rare (but see Gil et al. 1990). Food is more commonly associated with territory defense in insectivorous lizards (e.g., Simon 1975; Hews 1993) and territory size often tracks the trophic needs of the lizard (Stamps 1983). Even in complex social systems influenced by a variety of environmental and social factors, food abundance apparently plays some role (e.g., Ruby and Dunham 1987; M'Closkey et al. 1990a, 1990b). Among iguanids, however, food was the proximal target of male territoriality only in *Cyclura carinata* (Iverson 1979). Iguanids as a group spend little time foraging and are inactive and presumably thermoregulating during the majority of their aboveground activity (Carothers 1983; Gier 1997; van Marken Lichtenbelt et al. 1997). Such extended thermoregulation may be necessary for digestion of plant matter, because assimilation efficiencies in iguanids are low and high body temperatures increase food passage rates (Zimmerman and Tracy 1989). Thus, a physiological constraint may be the indirect cause of extended periods of female inactivity near the burrow entrance, which promotes male defense of those areas.

The reliance on burrows also influences the degree of local mate competition. In many populations of Ctenosaura and S. obesus, adequate shelters are so widely spaced that female home ranges overlap extensively around burrow entrances, leading to intense local mate competition among males. This has led to three-tiered male dominance hierarchies (Evans 1951; Berry 1974; Carothers 1981; Gier 1997), which have not been reported in insectivores. Thus, iguanids are unique as a group in that shelters often play a central role in movement patterns, and often lead to intense levels of local mate competition.

Although the importance of burrows in structuring the social system is clear in some species, the proximate benefit of the burrows may not be restricted to predator escape. They may also serve as refuges from extreme heat (as in D. dorsalis; Norris 1953) or as sleeping sites (Conolophus spp., P. Stone, pers. comm.). Few iguanids use permanent home burrows for oviposition, however, usually digging separate burrows, often some distance from the home burrow (e.g., Amblyrhynchus, Boersma 1983; Conolophus, Christian and Tracy 1982; Werner 1982; and Ctenosaura, Mora 1989).

In examining the hypothesis that iguanid mating systems are largely dependent on proximity to refuges from predation, the most instructive examples are those species that have lost that dependence, either by living in environments that offer many avenues of predator escape (i.e., I. iguana) or by evolutionarily "escaping" predation on islands. In fact, the only departure from RDP in a mainland form occured in I. iguana (figs. 1, 2).

The rest of the non-RDP species are insular endemics which suffer low predation rates as adults. Among the the Galapagos genera *Conolophus* and *Amblyrhynchus*, for example, predation on adults is very low (Galapagos hawks occasionally take gravid female *A. cristatus*; Boersma 1983) to nonexistent (adult *Conolophus* have no native predators; P. Stone, pers. comm.). Similarly, *Sauromalus varius* and *S. hispidus* are the largest terrestrial vertebrates on the xeric islands they inhabit (Case 1983). For either mainland or insular species, the absence of a reliance on localized shelters seems to act as a release, allowing alternative mating systems to evolve; this points to the importance of predation pressure in social evolution in this group. However, while the trend of low predation leading to non-RDP mating systems is suggestive, it is not unequivocal. The insular genera *Cyclura* and *Conolophus* still utilize RDP (fig. 2).

The evolution of leks in *A. cristatus* and *I. iguana* presents an interesting case for the importance of environmental factors impinging on female movements. In *A. cristatus*, terrestrial predation on adults is rare (Carpenter 1966; Boersma 1983) and the intertidal feeding areas are not defendable by males. In the riparian-arboreal habitat of *I. iguana*, individuals escape terrestrial predators by climbing trees and arboreal predators are avoided by jumping from branches into the water below. As in *A. cristatus*, feeding sites are not defendable, although in *I. iguana* this is due to the widespread availability of food. These environments have allowed relatively wide-ranging female behavior, which renders RDP an untenable strategy for males. The influence of harassment from subadult males (a common feature of many iguanid systems) may also contribute towards canalizing social evolution of these species toward the development of leks (Clutton-

Brock et al. 1992; Nefdt 1995). Harassment plays a role in driving female preference towards mating with large males, because once in their defended areas, they escape costly harassment from smaller males. Wikelski et al. (1996) observed that female harassment by low-rank males was lower for female A. cristatus within the lek. Similarly, female I. iguana outside the territories of the largest males were frequently the target of forced copulations by smaller males (Rodda 1992).

In summary, the evolution of large body size in iguanids has, at least for mainland forms, led to a reliance on substantial, often permanent shelters to allow escape from predators. Large body size therefore tends to drive iguanid social systems in a way unique among lizards. Conversely, the absence of reliance on localized shelters in arboreal or insular species may free them to more wide-ranging movement patterns than insectivorous iguanians due to a food supply which is generally more ubiquitous. Such a lack of dependence on clumped shelter, together with an absence of defendable feeding sites, may have been a key factor in the evolution of leks in I. iguana and A. cristatus.

The evolution of sexual dimorphism

If intrasexual interactions are primarily responsible for the evolution of head allometry in male iguanids (Carothers 1984), and since mating systems in part determine the nature of male-male interactions, head dimorphism patterns should coevolve with mating systems. There is no evidence of this, at least not at the limited level of analysis allowed by the data (fig. 2). There is no correspondence between mating system and the presence of head dimorphism. Similarly, there is no clear link between the evolution of dispersed shelters and simultaneous change in sexual dimorphism. However, a more firm conclusion regarding mating systems and sexual dimorphism will have to await morphological data on more genera. In particular, the exclusion of the genera Cyclura and Amblyrhynchus (due to unavailability of data) limits the usefulness of Fig. 2 as a tool for understanding the coevolution of ecology, behavior, and morphology in this group. Also, the role of head dimensions in female mate assessment in lekking species is unknown.

The phylogenetic contrast analyses examine the following questions: 1) can the two head dimorphisms (HC and HL) evolve independently; i.e., are there patterns in the evolution of HL dimorphism that occur independently of evolution of HC dimorphism?; and 2) can head dimorphism evolve independently of body size dimorphism? A curious result of the contrast analyses is the apparent decoupling of the different measures of sexual dimorphism. In the case of evolution of dimorphism in HL and HC (fig. 3), the significant relationship reveals that the two measures of head size track each other to some extent, but the scatter in the data indicates that evolution of one aspect of head morphology is not closely constrained by evolution of the other. Possibly these two aspects of male morphology are under the influence of different selection regimes; however, a more complete sample size is necessary to clarify the trend.

Relative head size determines the outcome of male-male interactions in some insectivorous lizards (Hews 1990; Vitt and Cooper 1985; Olsson 1992). Observations of male-male combat in iguanids, in which the head is used as a weapon (e.g., Iverson 1979; Gier 1997), suggest that evolution of head dimorphism in some species may be largely due to intrasexual selection. If true, different forms of male assessment or combat may exert different selective pressures on male head allometry, emphasizing head circumference in those species that engage in biting fights (e.g., Dipsosaurus dorsalis; Norris 1953; Gier 1997) and head length in those species that engage in gaping contests (e.g., Cyclura and Ctenosaura species; Iverson 1979; Gier 1997). However, the degree to which female choice plays a role, especially in lekking species, has not been investigated. Clearer understanding of the tie (if any) between sexual dimorphism and lizard mating systems requires more detailed studies of the role played by female choice of male quantitative characters, which is generally considered a rare phenomenon in lizards (Olsson and Madsen 1995; Tokarz 1995).

The absence of relationships between evolution of head dimorphism and that of MFR (fig. 4) is somewhat unexpected, since the nonindependence of the different variables (MFR and HL, in particular) increased the likelihood of finding a positive relationship. The scatter in these data suggest that the factors influencing relative body length of males and females are different from those governing the evolution of head dimorphisms. Possibly we are seeing the results of different selective agents; hypothetically, sexual selection could be the agent of change in head dimorphism whereas MFR may be influenced more by survivorship and/or fecundity. One confounding factor is that body size in this group is expected to be affected by the inclusion of both mainland and insular forms, since insularization in reptiles often leads to the evolution of gigantism (Case 1982, 1983). The extent to which males and females respond differently to insularization, if any, is not known.

One limitation of the present study is the difficulty in assigning species to an ecological category, since intraspecific variation may exist for the factor in question. Sauromalus obesus, for instance, exhibits some variation in the degree to which retreats are clumped, and in details of the nature of head dimorphism (C. Tracy, pers. comm.). Also, analyses such as these are hampered in that they rely on a wealth of basic data ranging from that which is difficult to quantify (e.g., the distribution of resources and their respective influences on animal movements) to that which is often considered unworthy of notice (e.g., the precise nature of male-male combat). Many clues to understanding the evolution of mating systems and sexual dimorphism in iguanids may also lie with the great number of species which remain poorly understood, particularly the majority of Ctenosaura and Cyclura species, as well as the genus Brachylophus.

CONCLUSIONS

The Iguanidae is a small family of lizards that exhibit a suite of behavioral features unique among lizards. First, they exhibit three distinct mating systems, one of which (leks) does not occur in any other reptile group. Second, among those species that exhibit RDP, groups of individuals are often very widely scattered and often are associated with three-tiered male hierarchies. These social systems, some of which are more similar to bird and mammal mating systems than to most other reptiles, appear linked to permanent shelters. Thus we have the seeming paradox of a group of lizards which by virtue of their large size should be less constrained by predation than smaller species, but in fact are more closely tied to structurally complex microhabitats that offer shelter. Another ecological distinction between herbivorous lizards such as iguanids and insectivores is the different dispersions of food supplies; in those iguanids for whom predator refuges are not limiting (either owing to the widespread nature of retreats, or to a lack of predation on insular species), food may play a lesser role in social system evolution than it does for insectivores. However, few studies have quantified the roles of these resources in determining individual movement patterns, and these conclusions are therefore tentative.

No broad parallels between mating systems and sexual dimorphism are revealed by these data. Two patterns suggest that sexual dimorphism in this family evolves in a complex fashion. First, dimorphisms in head length and head width do not coevolve tightly; some species appear to show the results of past selection on head length, and others on head circumference. Second, there is no link between the evolution of body length dimorphism and head size dimorphism. This complexity underscores the challenge of studying the coevolution of ecology, behavior, and morphology; however, as the group the iguanids may prove valuable as model systems for such studies in the future.

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Table 1. Social system characterization and dimorphism (differences between the sexes in the slope of the log-transformed head variable versus body length) in male-female head circumference (HC) and head length (HL) for members of the family iguanidae for which social organization and mating systems have been described. See Methods for mating system designations (RDP = resource defense polygyny; Mono = monogamy/ polygynandry). Defended resource is the object of male territoriality; bur = areas around shelter (burrows, crevices, etc.). Refuge clumping is a qualitative index of the degree to which predator refuges are aggregated in space; C = highly clumped; D = dispersed; M = moderate; parentheses indicate uncertain categorization.

Species	Mating system	Defended resource	Refuge clumping	HC dimorph	HL dimorph	References
Dipsosaurus dorsalis	RDP	?	M	0.095	0.051	Krekorian 1976; Alberts 1993
Conolophus subcristatus	RDP	bur	C	0.240	0.089	Werner 1982
Conolophus pallidus	RDP	bur	(C)	0.523	0.541	Christian & Tracy 1982
Amblyrhynchus cristatus	Lek	none	D	-	-	Carpenter 1966; Trillmich 1983; Boersma 1983; Rauch 1985; Wikelski *et al.* 1996
Sauromalus obesus	RDP	bur	C	0.409	0.224	Johnson 1965; Berry 1974; Ryan 1982; Prieto and Ryan 1978

Table 1 continued.

Species	Mating system	Defended resource	Refuge clumping	HC dimorph	HL dimorph	References
Sauromalus hispidus	Mono	none	D	0.038	0.056	Case 1982; Smits 1985
Sauromalus varius	Mono	none	D	0.289	0.093	Case 1982
Iguana iguana	Lek	none	D	0.522	0.210	Dugan 1982; Rodda 1992
Cyclura carinata	RDP	food/bur	M	-	-	Iverson 1979
Cyclura cornuta	RDP	bur	(C)	-	-	Dugan and Wiewandt 1982
Ctenosaura similis	RDP	bur	C	0.336	0.216	Henderson and Fitch 1979; Gier 1997
Ctenosaura hemilopha	RDP	bur	C	0.184	0.149	Carothers 1981
Ctenosaura pectinata	RDP	bur	C	-	-	Evans 1951

NOTE - all head dimorphism data from Carothers (1984).

FIGURE LEGENDS

Figure 1. Alternative phylogenies (Sites et al. 1996) for members of the family Iguanidae for which information on mating system and distribution of shelter is known. Black bars indicate clumped shelter; gray bars represent an intermediate level of shelter clumping; open bars represent dispersed shelters. Mating systems are classified as resource defense polygyny (R), leks (L), or monogamy/polygynandry (M). Horizontal bars indicate major changes in overall body size. Asterisks (*) indicate species endemic to islands. Di = Dipsosaurus; Co = Conolophus; Am = Amblyrhynchus; Sa = Sauromalus; Ig = Iguana; Cy = Cyclura; Ct = Ctenosaura.

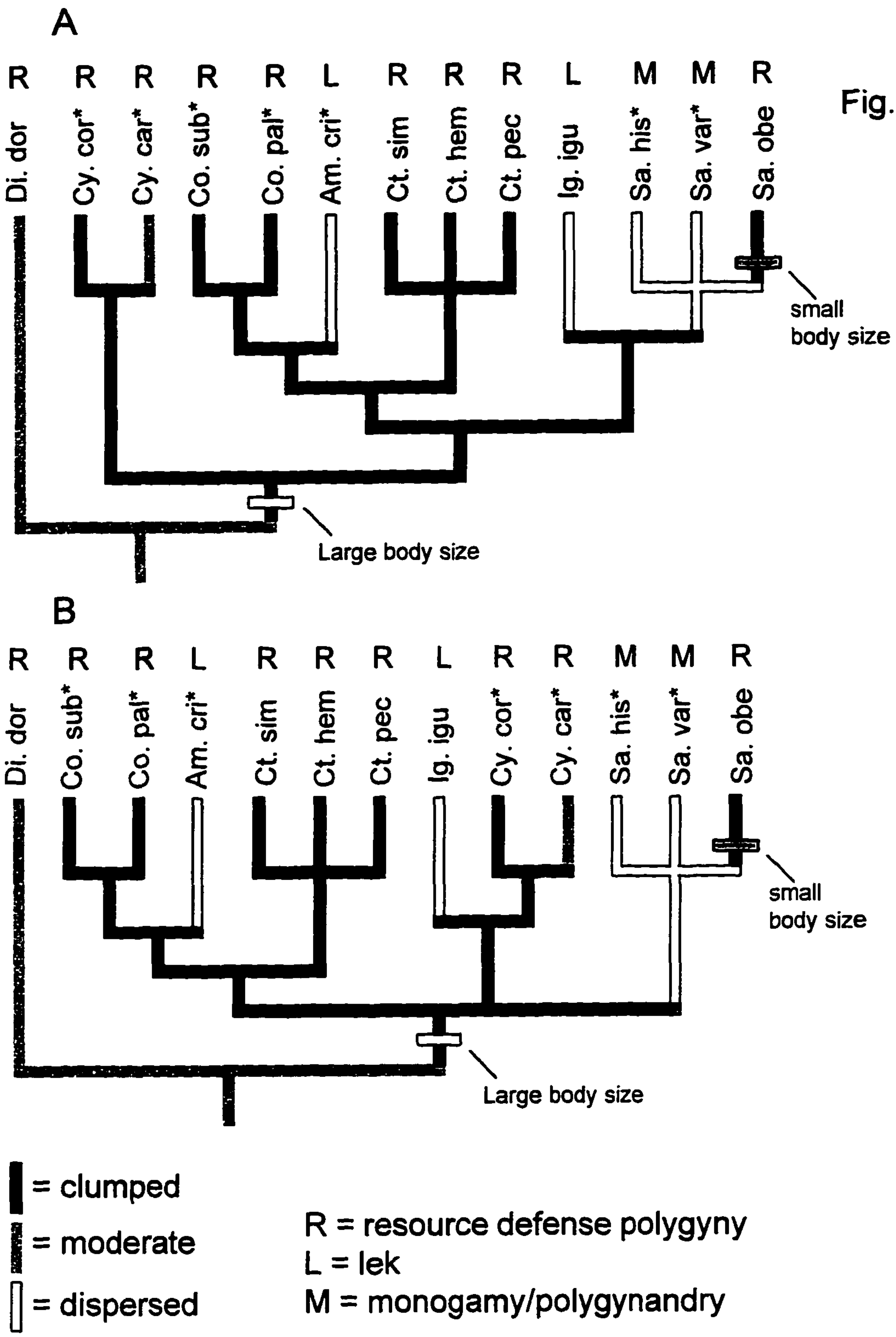
Figure 2. Alternative phylogenies (Sites et al. 1996) for members of the family iguanidae for which data on sexual dimorphism in head dimensions is available. Circles represent head circumference; squares represent head length. Filled symbols indicate a statistically significant difference in male and female head dimension allometry ($p < 0.05$). Numbers refer to between-node contrasts on values of head dimorphism shown in figs. 3 and 4. As in fig. 1, black bars represent clumped shelters; gray bars represent intermediate refuge clumping; open bars represent dispersed shelters. Mating systems are classified as resource defense polygyny (R), leks (L), or monogamy/polygynandry (M), and asterisks (*) indicate species endemic to islands.

Figure 3. Phylogenetic contrasts in male-female dimorphisms in head length (HL) versus head circumference (HC) for the node pairs indicated in fig. 2A.

Figure 4. Phylogenetic contrasts in male-female dimorphisms in head circumference

(HC) and head length (HL) versus phylogenetic contrasts in the ratio of male to female SVL. Numbers refer to node pairs indicated in fig. 2A.

Fig. 1


A
R R R R R L R R R L M M R
Di. dor
Cy. cor*
Cy. car*
Co. sub*
Co. pal*
Am. cri*
Ct. sim
Ct. hem
Ct. pec
Ig. igu
Sa. his*
Sa. var*
Sa. obe
small body size
Large body size
B
R R R L R R R L R R M M R
Di. dor
Co. sub*
Co. pal*
Am. cri*
Ct. sim
Ct. hem
Ct. pec
Ig. igu
Cy. cor*
Cy. car*
Sa. his*
Sa. var*
Sa. obe
small body size
Large body size
▮ = clumped
▨ = moderate
▯ = dispersed
R = resource defense polygyny
L = lek
M = monogamy/polygynandry

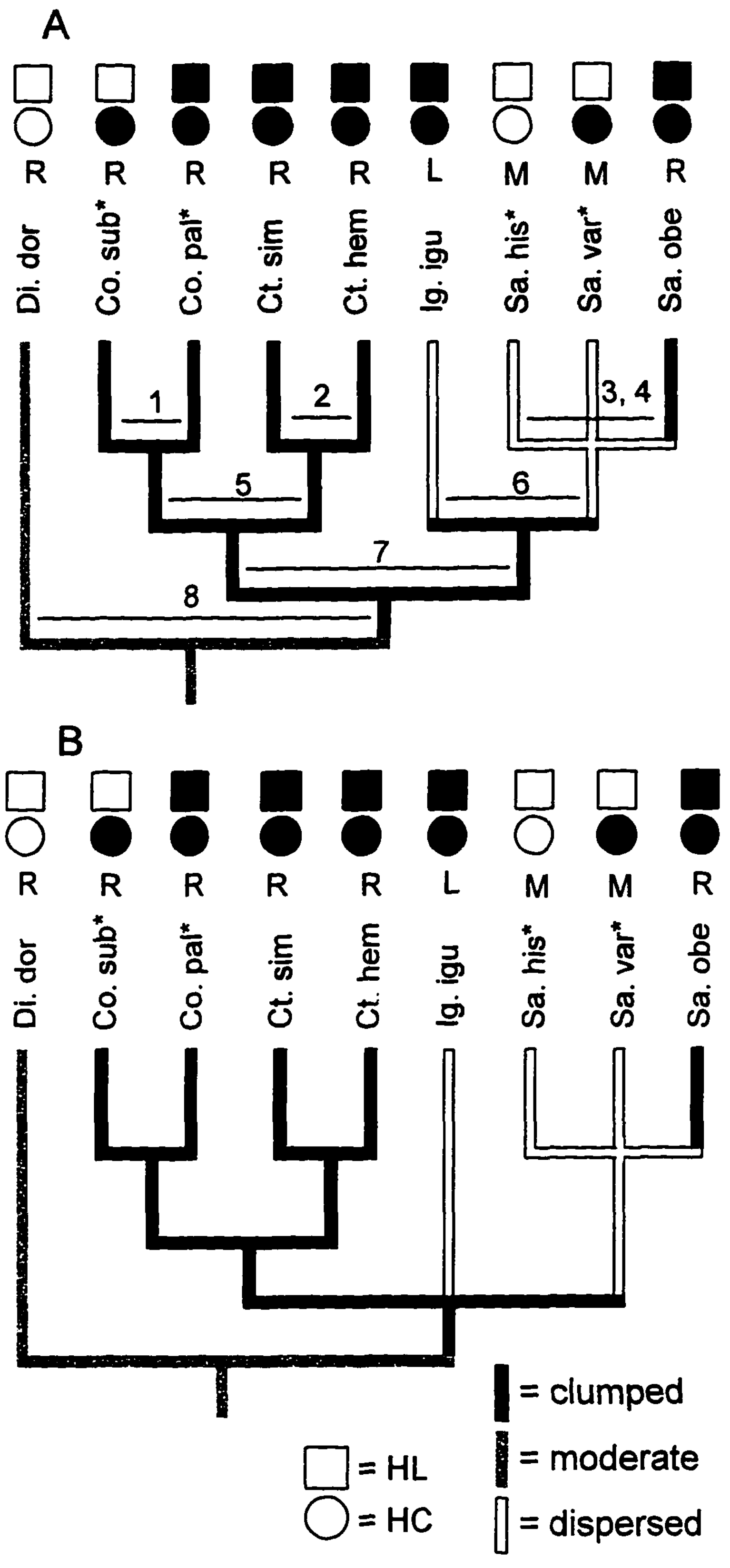

A
R
R
R
R
R
L
M
M
R
Di. dor
Co. sub*
Co. pal*
Ct. sim
Ct. hem
Ig. igu
Sa. his*
Sa. var*
Sa. obe
1
2
3, 4
5
6
7
8
B
R
R
R
R
R
L
M
M
R
Di. dor
Co. sub*
Co. pal*
Ct. sim
Ct. hem
Ig. igu
Sa. his*
Sa. var*
Sa. obe
= clumped
= moderate
= dispersed
= HL
= HC

Fig. 2

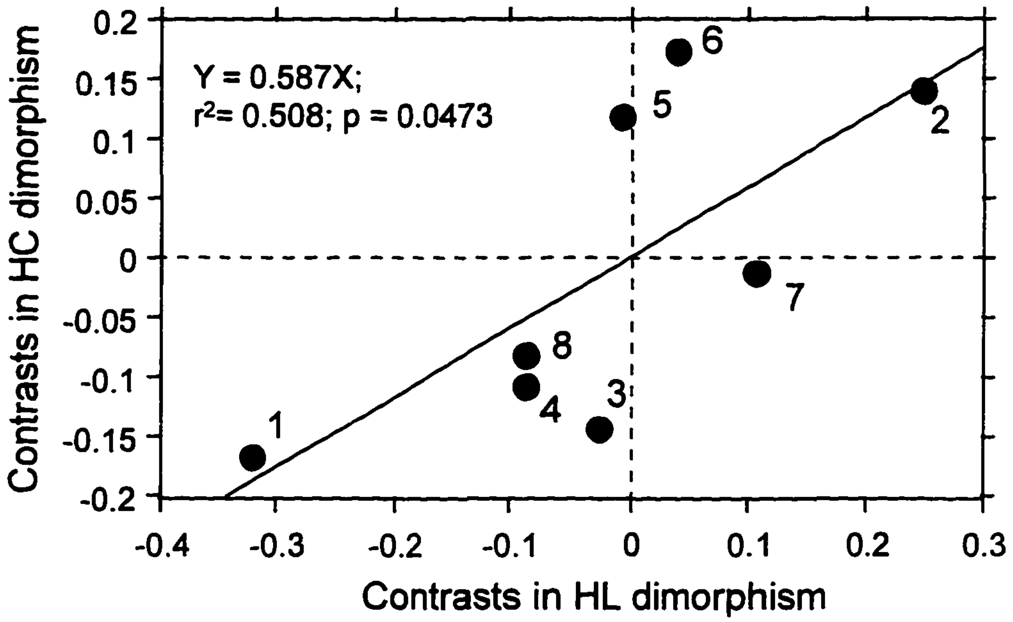
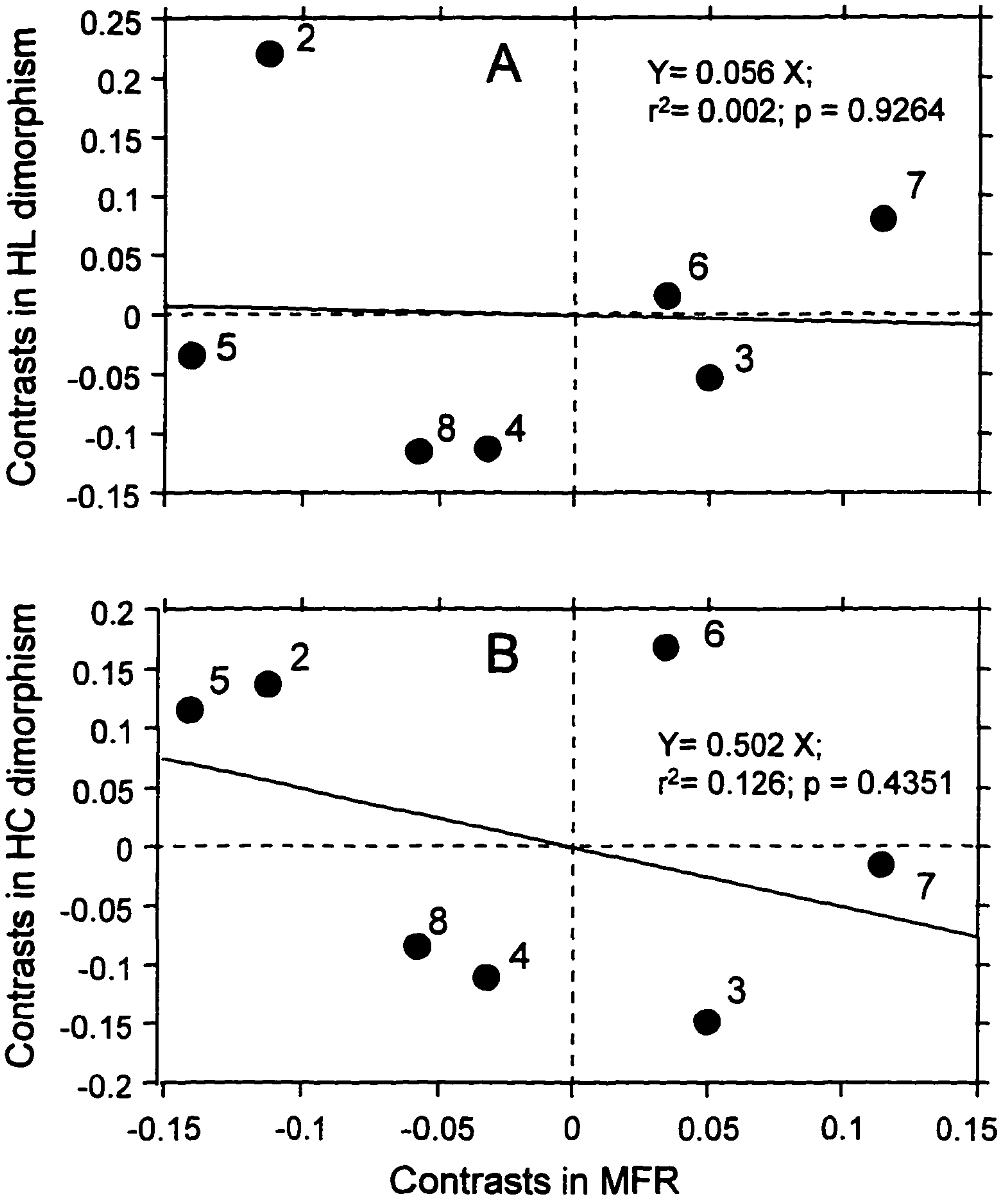

Y = 0.587X;
r^2= 0.508; p = 0.0473
Contrasts in HC dimorphism
Contrasts in HL dimorphism
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
1
2
3
4
5
6
7
8

Fig. 3

Fig. 4


A
Y= 0.056 X;
r^2= 0.002; p = 0.9264
Contrasts in HL dimorphism
0.25
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
2
5
8
4
6
3
7
B
Y= 0.502 X;
r^2= 0.126; p = 0.4351
Contrasts in HC dimorphism
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
5
2
6
7
8
4
3
-0.15
-0.1
-0.05
0
0.05
0.1
0.15
Contrasts in MFR