Habitat use, territoriality, and competitive interactions in Urosaurus ornatus (Sauria: Iguanidae) in southeastern Arizona.

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HABITAT USE, TERRITORIALITY, AND COMPETITIVE INTERACTIONS IN *UROS AURUS ORNATUS* (SAURIA: IGUANIDAE) IN SOUTHEASTERN ARIZONA

C. By Keith Andrew Baia

A Thesis submitted to the Faculty of Graduate Studies and Research through the Department of Biology in Partial Fulfillment of the requirements for the Degree Master of Science at the University of Windsor

Windsor Ontario, Canada 1986
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For my Family
ABSTRACT

Habitat use and territorial behaviour of tree lizards (*Urosaurus ornatus*: Iguanidae) were studied in riparian and flatland desert habitats at the Saguaro National Monument, Rincon Unit, Arizona, during spring and summer (March-August) 1984 and (May-August) 1985. Arthropod density increased 3.5-fold and 1.5-fold in the wet season during 1984 and 1985, respectively, did not differ between habitats, and was significantly higher in 1984 than 1985.

Males defended territories four times larger than those of females and occupied more trees than did females. Frequency of lizard activity at different locations within trees was unrelated to food density. There was no difference in arthropod density between territories of different sexes or between occupied and unoccupied trees.

Intraspecific territorial aggression among *U. ornatus* was assessed. It was predicted to decline as the breeding season terminated. Territorial behaviour did not cease as predicted, indicating the importance of territories for something other than food and mates.

Interspecific competitive interactions between *U. ornatus* and other iguanid lizards (*Sceloporus magister*
and *S. clarkii*) were assessed. There was a positive association in the local distribution of tree lizards and spiny lizards. However, there was no reduction in growth rate or residency time of *U. ornatus* living in association with spiny lizards. In experimental enclosures, the presence of spiny lizards had no effect on either *U. ornatus* residency time or feeding rate. There was no evidence for any competitive interactions with *Sceloporus* spp.
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Introduction

The spatial distribution of organisms among habitats is restricted by both biotic and abiotic factors. Throughout the range of a population, these factors will influence the quality and distribution of suitable habitats to which the animals have access. Therefore, habitats or patches may differ with some having higher quality than others. Habitat selection will result from the ability of an individual within a population to discriminate among available habitats.

The quality of habitats is undoubtedly influenced by many factors including population density, food resources, mate availability, vegetative cover, and other physical features. In addition, competitors and predators may lower habitat quality. An individual foraging in a favourable habitat may spend less time in that patch as a consequence of risks due to competitors or predators. As a result of this pressure, energy intake may be reduced, ultimately lowering individual growth rate and potential for survival. Habitats of highest quality should favour the greatest individual survivorship and reproductive success.

Among vertebrates, selection of a habitat involves an active choice by an individual in response to some environmental factor. The proximal cue may include
prey and mate availability, competitor and predator density, and environmental conditions (Davies and Houston 1984, Christian et al 1983, Emlen and Oring 1977). If habitat selection is adaptive, it will enhance an individual's chance to survive and reproduce.

The quality or suitability of habitats (Fretwell and Lucas 1969, Davies and Houston 1984) within an organism's range varies and individuals may exhibit choice in habitat colonization. Under ideal free conditions (Fretwell and Lucas 1969) individuals should first select or colonize the best quality patches of habitat. Individuals using such habitats may have a selective advantage over those in lower quality habitats. Individuals in better habitats may experience higher feeding rates, growth and reproduction, and they may have more mating opportunities (Kodric-Brown and Brown 1984, Ruby 1984, Emlen and Oring 1977, Fretwell and Lucas 1969). Consequently, fitness is higher for individuals selecting those habitats. As the effects of crowding become apparent, newly arriving individuals should settle in suboptimal but less crowded habitats. By doing so, these individuals may have fitness equivalent to those in better quality, but more crowded habitats. Therefore, distribution of individuals within a
population should reflect the differential quality of habitats.

Studies of lizard habitat utilization have been concerned primarily with the role of body size (Schluter 1984, Christian and Waldschmidt 1984), social behaviour (Stamps 1977), food availability (Simon 1978), and the effect of climatic conditions (Christian and Tracy 1985). Most lizards are insectivorous. A few are herbivorous or carnivorous (Rand 1967, Pianka 1975). The habitats occupied, times of activity, and foraging capabilities will influence the prey types available to lizards. Those lizards with specialized diets appear to be restricted to more specific habitats or patches than are generalized feeders. The horned lizard (*Phrynosoma* spp.) is an ant specialist and is restricted by the distribution of ant colonies (Munger 1984). At the other extreme, whiptail lizards (*Cnemidophorus* spp.) are free-ranging, eat a wide variety of foods, and may be restricted by some factor other than food resources. In contrast, iguanid lizards are territorial (Rand 1967). Territorial behaviour is a means by which acquisition of resources is insured. Individuals may increase their fitness by maintaining exclusive use of a territory (Davies and Houston 1984).

One goal of my work is to investigate patterns of
habitat use in the tree lizard, *Urosaurus ornatus* (Iguanidae), an insectivorous, territorial lizard. *Urosaurus ornatus* is found in dense, localized populations and the individuals within the population do not move great distances. Therefore, detailed movements and behavioural interactions are readily observed and individual territories can be relatively easily circumscribed. In addition, *U. ornatus* are easily captured to allow any manipulations or measurements. Earlier research has shown that *Urosaurus ornatus* population density differs between riparian and flatland habitats at the Saguaro National Monument, southeastern Arizona, U.S.A. I investigated the possible role of resource abundance in determining this distribution. Both overall habitat quality and *U. ornatus* territory quality were assessed by measuring arthropod density.

Economic defendability of resources is necessary for the expression of territorial behaviour (Brown 1964). Important resources include food, mates, oviposition or nesting sites, and refuges from predation (Davies and Houston 1984, Stamps and Tollestrup 1984). The importance of these defended resources may differ for the sexes. Male defense strategies include defense of habitats containing resources preferred or required by females, and defense
of females themselves (Stamps 1977, 1983, Davies 1978, Davies and Houston 1984, Emlen and Oring 1977). Females may select and defend territories on the basis of male quality or the resource quality within the habitat defended by the male (Hurly and Robertson 1985, Houston and Davies 1984).

The distribution, density and quality of resources will influence the value of a territory. Territorial behaviour may determine the spatial relationships and social organization of individuals within a population (Emlen and Oring 1977, Davis and Ford 1983, Davies and Houston 1984). Emlen and Oring (1977) postulated that the density and distribution of resources may affect the mating system by determining the aggregation of mates and the potential for monopolization of mates by territory holders. Territoriality should occur when the benefits received from such behaviour exceed or at least equal the costs incurred from defense (Davies and Houston 1984). The benefits of defending a territory increase as territory size increases to an area beyond which further increase in resources will bring no additional benefits to the individual. At the same time, costs increase as territory size increases due to the greater amount of time an individual would have to allocate to patrol and defend a larger territory. The territory model predicts that the optimal territory
size maximizes the difference between the benefits and costs (Davies and Houston 1984).

Territory size is expected to have an inverse relationship with territory quality. Kodric-Brown and Brown (1978) found this relationship to hold for rufous hummingbirds as the bird's nectar supply fluctuated within defended territories. Stamps (1983) found the prediction to hold for juvenile *Anolis aeneus* lizards due to predator risk. Both studies reveal changes in territory size as the benefits of territory defense changed.

Another goal of my thesis was to investigate territory characteristics of *Urosaurus ornatus*. Individual territories are discernable from mark-recapture census data. I defined territory size and compared this between sexes. The variation in territory size and abundance of resources are investigated.

Access to preferred habitat types may be constrained for some individuals within a population, due to the presence of competitors (MacArthur 1972). Occupation of a site by a territorial resident may preclude establishment of invaders or invasion of the site by newly arriving individuals. Krebs (1971) found that great tits preferred woodland sites, which correlated with superior breeding success, but some
individuals were forced to inhabit a less preferred hedgerow where breeding success was reduced. The territorial behaviour of resident great tits prevented the invasion of other individuals into higher quality preferred habitat.

Due to their status in the population, some individuals may not have access to high quality habitats. This has been reported in many populations with dominance hierarchies. Status of individuals has been found to be associated with age, sex, and residency. Fox (1983) found dominant Uta stansburiana to successfully defend higher quality home ranges, based on predator refuges, from invasion by subordinates. Stamps (1983) provided experimental evidence that dominant individual Anolis aeneus lizards successfully defended predator refuges from subordinates. In this instance, dominance was associated with both age and body size. Ruby (1984) reported evidence that territorial behaviour in Anolis carolinensis allows larger heavier males greater mating success than smaller individuals. Results of these and other studies clearly indicate that individuals within a population do not have equal access to all habitats or resources. Equal access is an assumption of the Fretwell-Lucas model (1969) of habitat use.

My observations on tree lizards revealed intense
intraspecific territorial aggression among males. This behaviour suggests that maintenance of exclusive territories is an important life history feature of *U. ornatus*. Experimental introductions of non-resident lizards were conducted to assess the aggressive behaviour of resident males during and after the breeding season. I investigated the role of body size in the introduction experiments.

The importance and influence of competitors within and between species have been invoked as a major determinant of species distribution and community structure (MacArthur 1972, Strong et al 1984). Most studies of interspecific competition in lizard communities have been comparative and have provided support for the view that interspecific competition determines many of the patterns observed in lizard communities. There have been few experimental studies of lizard communities to examine interspecific competition (Dunham 1983).

In order for competition to occur, individuals must utilize some common resource which must be in limited supply. Consequently if competitors co-exist the available resources must be shared among them or one competitor may be excluded from that resource. Evidence to suggest that competition is occurring would include reductions in growth rates, population density,
feeding efficiency, feeding rate; or a change in the local distribution of individuals.

Lizards are ideal organisms to investigate the consequences of competition. Growth rates are easily acquired by obtaining snout-vent lengths throughout the study period. Population densities and distributions are readily monitored and manipulated. Because the lizards are diurnal, behavioural interactions are readily quantified and feeding rates easily monitored.

Interspecific competition imposes costs to an individual engaged in territory defense. The density of competitors and the competitive ability of individuals will influence the defense of territories and selection of habitats. In studies of Anolis lizards, Pacala and Roughgarden (1984) found evidence that perch sites were limiting resources. They found that the Anolis spp. shifted their time and location of activity due to the presence of competitors. Survivorship was lower in the presence of competitors (Smith 1981) and Pacala and Roughgarden (1985) found reduced growth rates, smaller volumes of developing eggs per female, smaller volumes of arthropods per lizard, and smaller mean prey sizes when two Anolis spp. were in sympathy.

The effects of competition may be ephemeral as Dunham (1980) found with Sceloporous merriami and Urosaurus ornatus. Competition had significant effects
only in the two dry years of a four-year study. The results of this study indicate that these species compete significantly during periods of drought induced food scarcity, and not at other times suggesting that prey is periodically limiting. These studies show that competition may not always occur, indicating the importance of long-term studies. I observed *U. ornatus* and yearling spiny lizards co-occurring on mesquite trees. As a fourth part of my thesis I investigated the possible role of interspecific competition in determining *U. ornatus* distribution and growth. Growth rates of *U. ornatus* were compared in the presence and absence of spiny lizards. In experimental trials, *U. ornatus* feeding rates and behaviour were assessed in the presence and absence of spiny lizards.

*Urosaurus ornatus* is widespread in the deserts of the southwestern United States. Life history traits and demography have been reported by several authors (Ballinger 1976, 1977, 1984, Dunham 1980, 1981, Tinkle and Dunham 1983). The reproductive biology of the tree lizard has been studied in different geographical locations (Asplund and Lowe 1964, Martin 1973, 1977, Ballinger 1977, Dunham 1981, Tinkle and Dunham 1983), and both the duration of the breeding season and clutch frequency are known to vary. Resource availability has been shown to be an important factor in *U. ornatus*
habitat use (Vitt et al. 1981).

Standard mark-recapture surveys and experimental manipulations were done to study habitat use, territoriality, and competition in Urosaurus ornatus. Field work was conducted in the lower Sonoran desert at the Saguaro National Monument, Rincon Mountain Unit, Arizona. Habitat use was compared between riparian and flatland habitats. Arthropod resource abundance was estimated and used as a measure of habitat quality.

I present an analysis of resource availability between habitats and among tree lizard territories. I present data on tree lizard territories and the territorial aggression of Urosaurus ornatus. Experimental and observational data were used to assess interspecific competition between the tree lizard U. ornatus and spiny lizard Sceloporus magister.
Study Site

Field work was conducted in the Lower Sonoran desert of Southeastern Arizona, at the Rincon Unit, Saguaro National Monument (Fig. 1). This desert is typified by a biseasonal regime of summer and winter precipitation (Lowe 1964). The study periods extended through the summer months, March-August, 1984, and May-August, 1985. The dry season is delineated by a spring-summer drought lasting from March through the end of June. The wet season extends from the beginning of July through September and is characterized by seasonal monsoons. Therefore, each field season included both a dry and wet season.

The study sites were adjacent to rocky bajadas on the western edge of the Rincon Mountains, the latter reaching an elevation of approximately 2623 m. The elevation of the study site is approximately 900 m. One site is riparian woodland habitat (Wash plot) located on a wash that bisects the Saguaro National Monument. The major vegetation is composed of paloverde (Cercidium microphyllum), mesquite (Prosopis juliflora), catclaw (Acacia greggii), and netleaf hackberry (Celtis reticulata). The trees and shrubs form a linear plot, 2 - 4 trees wide, with a continuous canopy. Fifty different mesquite trees were selected
Figure 1: Tree lizard (*Urosaurus ornatus* : Iguanidae) distribution (from Stebbins, 1980). Star represents field study location.
as sampling units on this plot, which covered approximately 0.4 ha.

The second plot was located in desert flatland habitat (Flatland plot) above and adjacent to the Wash plot. The major components of vegetation included foothill paloverde (*Cercidium microphyllum*), mesquite (*Prosopis juliflora*), saguaro (*Cereus giganteus*), creosote bush (*Larrea divaricata*), cholla and prickly pear (*Opuntia* spp.), barrel cactus (*Echinocactus* spp.), hedgehog cactus (*Echinocereus* spp.), ocotillo (*Fouquieria splendens*), brittle bush (*Encelia farinosa*), white-thorn acacia (*Acacia constricta*), and pin cushion cactus (*Mammillaria* spp.). Twenty-nine mesquite trees on this plot covered approximately 0.6 ha.

Lizard Fauna

Several different lizard species co-occur on these two study plots. The largest is the gila monster (*Heloderma suspectum*: Helodermatidae), which is relatively rare and usually found in flatland habitats. The ground-dwelling regal horned lizard (*Phrynosoma solare*: Iguanidae) inhabits both plots and the nocturnal banded gecko (*Coleonyx variegatus*: Gekkonidae), which is mainly saxicolous was rarely
seen. Ground-dwelling adult spiny lizards (*Sceloporus magister*: Iguanidae), are found in the flatland and the sub-adults inhabit mesquite trees in the wash. Clark's spiny lizard (*Sceloporus clarki*: Iguanidae) is restricted to mesquite trees in the wash and were never sighted in the flatland. Two other lizards, both ground dwelling, the greater earless, (*Cophosaurus texanus*: Iguanidae), and the zebra-tailed, (*Callisaurus draconoides*: Iguanidae), inhabit desert washes, but the former is also found on rocky bajadas, the latter in flatland habitats (Stebbins 1980). Two other ground-dwelling lizards found on both plots are the whiptails (*Cnemidophorus* spp: Teidae) and the side-blotched lizard (*Uta stansburiana*: Iguanidae), the latter only rarely seen in the study area. The most abundant lizard found on both plots, and the lizard under study, is the tree lizard (*Urosaurus ornatus*: Iguanidae) with an adult snout-vent length (SVL) of 40 to 60 mm (Stebbins 1980, Pers. obs.). *Urosaurus ornatus* inhabit mesquite trees on both the wash and flatland plots. They are also saxicolous (occupy rocky habitats). On my study sites rocky habitats were absent.
Urosaurus ornatus Life History

Urosaurus ornatus is a sexually dimorphic, territorial lizard. It is insectivorous, diurnal, and widespread over the southwest desert of the United States and Mexico (Stebbins 1980, Dunham 1982, Fig. 1). Throughout its range, it has been reported to be arboreal (Asplund 1964, Martin 1973, 1977, Michel 1976, Tinkle and Dunham 1983) as well as saxicolous (Asplund 1964, Martin 1973, 1977, Dunham 1980). In the Saguaro National Monument U. ornatus is both saxicolous and arboreal.

Hatchlings have a SVL of approximately 20-21 mm, and will reach maturity in their first year (pers. obs.). At my study site there is evidence of the production of 2 clutches a year: the first clutch is deposited by mid-July and hatchlings emerge in mid-August. The second clutch is deposited in late August and hatchlings emerge sometime in October.

The male testicular cycle begins in early April (Asplund and Lowe 1964, Michel 1976). The testes enlarge rapidly until mid-May and peak in size in July. At this time they begin to retrogress, and reach minimum size in October, remaining in this state until the following spring (Asplund and Lowe 1964).
Habitat Use

Introduction

The distribution of individuals within populations is usually determined by resources, including habitats, food, and mates, and by the presence or absence of competitors, and predators. Models of habitat and niche assume that there is variation in the quality and availability of resources within an organism's range or habitat (Fretwell and Lucas 1969). The theory of habitat selection predicts that individuals should first occupy habitats of highest quality. As the availability of these habitats decreases or the quality of these habitats declines, individuals should inhabit the next best habitat patch (Fretwell and Lucas 1969, Davies and Houston 1984). This implies that individuals can assess the quality of habitats and make choices based on the resources contained in the habitats. As a result the distribution of individuals within a population should reflect the availability and distribution of their vital resources.

Acquisition of resources may be associated with defense of a territory or occupation of a home range that insures an organism's access to resources (Davies and Houston 1981, Fox et. al. 1984, Rose 1982, Stamps
1983, Christian and Waldshmidt 1984, Hurly and Robertson 1984, 1985, Stamps and Tollestrup 1984, Ruby 1984, Smith 1985, Wolf 1985). Ferguson et al. (1983) demonstrated that food availability was a prime factor in the territorial behaviour of juvenile *Sceloporus undulatus*, and Stamps (1983) found that juvenile *Anolis aeneus* compete for home sites of complex topography which enhances predator avoidance. The quality of the habitat (territory or home range) occupied by an individual will be influenced by the population density in that habitat. The fitness of individuals within a high density high quality habitat may be equal to that of individuals in a poor habitat with low density (Emlen and Oring 1977, Davies and Houston 1984). Fox (1983) established that home range quality was greater for surviving than non-surviving *Uta stansburiana*. Individuals able to hold and defend territories may have greater longevity and as a result experience greater reproductive success.

Many investigators have focused on the availability of food resources as a major factor in determining species distribution (Davies and Houston 1981, 1984, Ferguson et al. 1983, Karasov and Anderson 1984, Christian and Tracy 1985, Stamps and Buechner 1985, Newton et al. 1986). One effect of territorial behaviour may be to insure that individuals within a
population are sufficiently dispersed to allow adequate resource acquisition. When resource levels are high, individuals may tend to decrease territory size and/or tolerate intruders. This results in higher territory overlap (Simon 1975, Davies and Houston 1984, Stamps and Buechner 1985). Thus, distribution patterns should reflect differences in resource abundance and availability.

The distribution of *Urosaurus ornatus* was assessed in the Sonoran Desert of southeastern Arizona by monitoring arthropod density throughout the spring and summer months (March-August, 1984; May-August, 1985). Arthropod density was assessed in a wash and flatland habitat during a dry and wet season to determine if *Urosaurus ornatus* distribution was dependent on food availability. Arthropod density was compared among lizard territories, and between occupied and unoccupied trees.

Arthropod density was assessed by using Tanglefoot™ traps. A drawback in using the Tanglefoot™ to capture arthropods is its inability to capture crawling insects such as ants, which are part of tree lizard diets (pers. obs., Asplund 1964, Vitt et al 1981). For this reason I accepted the tree estimates as representing minimum arthropod density. The order of arthropods represented on the Tanglefoot™
traps (pers. obs.) compared with those found in stomach analysis of *U. ornatus* (Asplund 1964).

Methods

Lizard Census

Censuses were conducted during both field seasons. Because *U. ornatus* is a diurnal ectotherm, censuses commenced by 0700 hr when both lizard activity and temperature were increasing. Peak lizard activity was early to mid morning. Lizards were captured on sight, by hand or noose, their sex determined, weighed (g), snout-vent length measured (mm), were paint marked for quick identification, and toe clipped for permanent identification. After processing, each lizard was released at the point of capture. During the 1984 field season on the wash, 9 complete censuses were conducted with a mean census interval of 11 days. On the flatland, 12 complete censuses were conducted with a mean census interval of 12 days.
Arthropod abundance

Arthropod density was estimated during 1984 and 1985. During 1984, estimates were obtained by positioning cards (15 cm²) 2 to 4 m from the base of each mesquite tree on both the wash and flatland plots, with the upper surface coated with an adhesive (Tanglefoot™) which immobilizes arthropods when they come into contact with it. Arthropod density was estimated during each month of the 1984 field season, (5 months), which was divided into a dry (April - June) and wet (July - August) season. The Tanglefoot™ cards were exposed for four consecutive days during each sampling period. There were 362 cards, 221 for the dry season samples (n = 143 wash cards, n = 78 flatland cards), and 141 cards for the wet season samples (n = 89 wash cards, n = 52 flatland cards).

After collecting the Tanglefoot™ cards, arthropods were identified to order. Length and width (mm) of each arthropod were recorded. The arthropods were grouped into size categories according to length (<1 mm, 1-2 mm, 2-4 mm, 4-8 mm, 8-16 mm, 16-32 mm).

To test the hypothesis that Urosaurus ornatus distribution and abundance were limited by arthropod food resources, a two-way analysis of variance was performed to compare arthropod density between the wash
and flatland during the dry and wet season.

Arthropod size distributions (arthropods size class$^{-1}$) in the dry and wet season were analysed by a two-factor ANOVA following a Box-Cox transformation of data ($\lambda = 0$, Sokal and Rohlf 1981) to determine if there was a differential seasonal increase in certain sizes of arthropods among habitats. The interaction test in the two-way ANOVA will detect a differential increase in the abundance of arthropods size class$^{-1}$, and the main effects are not of interest (Sokal and Rohlf 1981, Keppel 1982).

During the 1985 field season the same techniques were used with slight modifications. Arthropod density was estimated during both seasons with only one sampling period per season and only on the wash plot. Fifteen cards were placed on the ground during both the wet and dry seasons at regular intervals (10 m) on a line transect among the mesquite trees. In addition, arthropod density was sampled within the mesquite tree canopy. The cards were hung vertically, and held in position with wire between branches to allow maximum exposure. Seventy cards (3 per tree) were hung in the trees during both the wet and dry season. Excluding damaged or disturbed cards that did not allow arthropod identification, there were 82 cards in the dry season ($n = 69$ tree cards, $n = 13$ ground cards), and 81 cards
in the wet season (n = 66 tree cards, n = 15 ground cards). All cards were collected after a seven day exposure period. Arthropods were identified and classified according to methods used in 1984.

Wash mesquite trees were grouped as either occupied by territorial lizards or unoccupied to determine if the territories defended by individual *Urosaurus ornatus* differed in arthropod density. A tree was considered occupied if a lizard was found on that tree at least twice during a season.

The trees of the wash were divided on the basis of occupation by the different sexes and a two-way ANOVA performed on Box-Cox transformed data to distinguish any differences in arthropod density within territories defended by males and females.

A two-way ANOVA was performed using the 1985 arthropod density estimates to determine if differences existed between seasons, and to determine if there were differences between the tree and ground estimates.

Statistical analyses were performed in accordance with the procedures of Sokal and Rohlf (1981) and Keppel (1982). Analyses were executed with Statpro™ (Statpro 1984) on an IBM PC micro computer.
Results

A total of 384 and 57 U. ornatus were captured on the wash and flatland plots, respectively (Table 1). The wash supported a larger lizard population than did the flatland. Lizard densities (lizards tree\(^{-1}\)census\(^{-1}\)) were significantly higher on the wash plot than on the flatland plot \((t = 6.32, p < 0.001)\).

During 1984, 50,426 arthropods were identified. During the dry season 19,559 arthropods were counted, the wash and flatland represented 72% and 28% of the count, respectively. Wet season estimates included 30,867 arthropods, 58% on the wash and 42% on the flatland. Arthropod density between the two seasons differed \((F=34.054, p < 0.005, \text{Table 2, figure 2})\). The wet season estimate \((\bar{x} = 26.00\ \text{arthropods dm}^{-2}\text{day}^{-1})\) was significantly higher than the dry season estimate \((\bar{x} = 9.79\ \text{arthropods dm}^{-2}\text{day}^{-1})\). However, the arthropod density between the two habitats did not differ significantly \((F = 1.35 \times 10^{-5}, p > 0.75, \text{Table 2})\). Because Urosaurus ornatus densities were higher in the wash and the potential food resources did not differ between the two habitats, there is no indication that tree lizard distribution is related to arthropod density at the scale of different habitat types.
Table 1: Lizard census on the wash and flatland plots, 1984.

<table>
<thead>
<tr>
<th></th>
<th>Wash</th>
<th>Flatland</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total captures</td>
<td>384</td>
<td>57</td>
</tr>
<tr>
<td>Marked lizards</td>
<td>149</td>
<td>34</td>
</tr>
<tr>
<td>Lizard Recaptures</td>
<td>235</td>
<td>23</td>
</tr>
<tr>
<td>Number of Males</td>
<td>67</td>
<td>20</td>
</tr>
<tr>
<td>Male Recaptures</td>
<td>186</td>
<td>35</td>
</tr>
<tr>
<td>Number of Females</td>
<td>82</td>
<td>14</td>
</tr>
<tr>
<td>Female Recaptures</td>
<td>198</td>
<td>22</td>
</tr>
</tbody>
</table>
Table 2: Two-Factor ANOVA of arthropod density (arthropods dm\(^{-2}\)day\(^{-1}\)) during the dry and wet season between the wash and flatland habitats, 1984.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>1</td>
<td>630.893</td>
<td>34.054</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>Habitat</td>
<td>1</td>
<td>2.5 \times 10^{-4}</td>
<td>1.35 \times 10^{-5}</td>
<td>&gt; 0.75</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>41.168</td>
<td>2.222</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>Error</td>
<td>6</td>
<td>111.159</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>9</td>
<td>783.221</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2: Mean (± 1 S.E.) arthropod density (arthropods dm$^{-2}$day$^{-1}$) during the dry and wet season on the wash and flatland habitats, 1984.
The arthropod size distribution analysis revealed a significant difference in the abundance of arthropods between size classes. \( F=37.667, p < 0.001, \text{Table 3, figure 3} \). There were more small arthropods than large ones. A significant seasonal pattern was also apparent. Because there was no significant interaction \( F=1.414, p > 0.25, \text{Table 3} \) the different size classes of arthropods increased similarly between the dry and wet seasons. Therefore, the data suggest that the increase in arthropod numbers represents an increase in arthropod biomass.

The estimates of arthropod density on the occupied and unoccupied trees were not significantly different (\( F = 0.007, p > 0.75, \text{Table 4, figure 4} \). *Urosaurus ornatus* do not appear to be defending territories on the basis of arthropod density.

The territories defended by individuals of each sex or those that were defended by a male and female did not differ in arthropod density (\( F = 0.378, p > 0.75, \text{Table 5, figure 5} \)).

During the 1985 field season 10,149 arthropods were identified. The tree counts represent 73% of this total (\( n = 7,354 \) tree, \( n = 2,795 \) ground). The two-way ANOVA of the 1985 arthropod estimate reveals that there is a significant interaction (Table 6) so post-F simple effects tests were performed (Keppel
Table 3: Two-Factor ANOVA of arthropod size
distributions (arthropods size$^{-1}$ class
dm$^{-2}$day$^{-1}$) between the dry and wet season,
1984. A Box-Cox transformation (lambda = 0)
was performed to normalize the data.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
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</thead>
<tbody>
<tr>
<td>Season</td>
<td>1</td>
<td>6.755</td>
<td>14.365</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>Size class</td>
<td>5</td>
<td>88.567</td>
<td>37.667</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>5</td>
<td>3.324</td>
<td>1.414</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>8.465</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>107.111</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3: Mean (+ 1 S.E.) arthropod density (arthropods dm⁻² day⁻¹) within each size class during the dry and wet season. Box-Cox transformed data (λ = 0).
Table 4: Two-Factor ANOVA of arthropod density (arthropods dm$^{-2}$day$^{-1}$) on trees occupied by *Urosaurus ornatus* and those unoccupied on the Wash plot during the dry and wet season, 1984. A Box-Cox transformation ($\lambda=0$) was performed to normalize the data.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
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</thead>
<tbody>
<tr>
<td>Season</td>
<td>1</td>
<td>28.843</td>
<td>113.999</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Occupation</td>
<td>1</td>
<td>0.002</td>
<td>0.007</td>
<td>&gt; 0.75</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>0.026</td>
<td>0.101</td>
<td>&gt; 0.75</td>
</tr>
<tr>
<td>Error</td>
<td>228</td>
<td>57.687</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>231</td>
<td>86.558</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 4: Mean (± 1 S.E.) arthropod density (arthropods dm⁻²day⁻¹) on trees occupied and unoccupied by U. ornatus on the wash.
Table 5: Two-Factor ANOVA of arthropod density (arthropods dm$^{-2}$day$^{-1}$) on trees occupied on the wash plot by different sexes of *Urosaurus ornatus*, 1984. A Box-Cox transformation (lambda=0) was performed to normalize the data.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>1</td>
<td>28.843</td>
<td>114.067</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Sex</td>
<td>2</td>
<td>0.191</td>
<td>0.378</td>
<td>&gt; 0.75</td>
</tr>
<tr>
<td>Interaction</td>
<td>2</td>
<td>0.376</td>
<td>0.744</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>Error</td>
<td>226</td>
<td>57.147</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>231</td>
<td>86.557</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 5: Mean (+ 1 S.E.) arthropod density (arthropods \( \text{dm}^{-2} \text{day}^{-1} \)) on trees occupied by different sexes of \textit{U. ornatus}. 
1982, table 7). The results indicate the same seasonal trend exists in 1985 as in 1984; arthropod density differs between seasons with higher arthropod density in the wet season (figure 6), however arthropod density on the ground increased more than within the tree. The data reveal greater density of arthropods on the ground, in both seasons, than within the tree canopy (Table 6, figure 6). Therefore, tree estimates may represent a lower limit of arthropod food resources available to *U. ornatus*.

Arthropod density between 1984 and 1985 differed significantly (\( F = 77.275, p < 0.001, \) Table 8, figure 7). This suggests that 1984 was a better year for *U. ornatus* based on arthropod food resources.
Table 6: Two-Factor ANOVA of arthropod density (arthropods dm$^{-2}$day$^{-1}$) during the dry and wet season between the tree canopy and ground (location), 1985:

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
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</thead>
<tbody>
<tr>
<td>Season</td>
<td>1</td>
<td>72.875</td>
<td>31.436</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Location</td>
<td>1</td>
<td>219.994</td>
<td>94.877</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>10.595</td>
<td>4.570</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Error</td>
<td>159</td>
<td>368.595</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>162</td>
<td>672.008</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 7: Simple effects tests ANOVA table of arthropod density (arthropods dm^{-2}day^{-1}) during the dry and wet season between the ground and tree canopy, 1985. A represents season, A_1 represents the dry season, A_2 represents the wet season. B represents location, B_1 represents the tree, B_2 represents the ground.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>A at B_1</td>
<td>1</td>
<td>12.063</td>
<td>5.195</td>
<td>&lt; 0.025</td>
</tr>
<tr>
<td>A at B_2</td>
<td>1</td>
<td>65.298</td>
<td>28.119</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>B at A_1</td>
<td>1</td>
<td>64.66</td>
<td>27.844</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>B at A_2</td>
<td>1</td>
<td>159.894</td>
<td>68.854</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>159</td>
<td>368.495</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 6: Mean (± 1 S.E.) arthropod density (arthropods $dm^{-2}day^{-1}$) on the wash trees and ground in 1985.
Table 8: Two-Factor ANOVA of arthropod density (arthropods dm$^{-2}$day$^{-1}$) between 1984 and 1985. Ground arthropod estimates during both years were used in the comparison. A Box-Cox transformation ($\lambda=$0) was performed to normalize the data.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
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</thead>
<tbody>
<tr>
<td>Season</td>
<td>1</td>
<td>25.273</td>
<td>107.496</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>18.168</td>
<td>77.275</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>0.649</td>
<td>2.763</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>Error</td>
<td>256</td>
<td>60.188</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>259</td>
<td>124.279</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 7: Mean (± 1 S.E.) arthropod density (arthropods dm⁻² day⁻¹) during 1984 and 1985.
Discussion

The availability of food resources can vary temporally and spatially. The usual trend is that arthropod density is lower during dry periods. Numerous authors have investigated the consequences of temporal and/or spatial differences in prey availability on growth rates, body size, and reproductive output in lizard populations (Karasov and Anderson 1984). In a four year study, Dunham (1980) found that arthropod density was significantly lower in two dry years compared to two wetter years. Individuals of both lizard species studied experienced stressful conditions during the dry years as reflected by a significant reduction in foraging success, growth rate, body mass, prehibernation lipid level and population density. During these dry periods, limited resources lead to a presumed increase in competition resulting in lower fitness.

Arthropod density in 1984 showed strong seasonality. There was a greater density of arthropods after the commencement of the wet season. The summer rain triggered a 3.5-fold increase in arthropods on the flatland plot and a 2-fold increase on the wash plot. Others have observed similar patterns of insect abundance and moisture level (Hadley and Szarek 1981,
Dunham 1980, Stamps 1977, Buskirk and Buskirk 1976, Janzen and Schoener 1968). Despite this seasonal pattern there was no significant difference between the two habitats studied. Janzen and Schoener (1968) found insect abundance to be significantly different on adjacent plots, however, these plots differed in their moisture regime.

It stands to reason that if animals do so poorly during dry periods if resources are limiting, then the time for optimal growth and reproduction would be during the wet periods of abundant resources. However a substantial proportion of U. ornatus growth occurs, and females are gravid with their first clutch when resources are most limiting (pers. obs.). Urosaurus ornatus numbers decline as the season progresses. Lizard density does not increase until juvenile recruitment occurs in late August. Recruitment corresponds with the increase in arthropod abundance.

Lizard density was higher on the wash plot during both seasons. Yet arthropod density did not differ between habitats. A model of habitat quality (Fretwell and Lucas 1969, Davies and Houston 1984) predicts a greater density of individuals in areas of better quality resources. This suggests that arthropod density may not be an important determinant of habitat quality in U. ornatus. Some other resource may limit
U. ornatus numbers. Stamps (1983) also found that territories were not defended on the basis of food, but defense was related to refuges from predation. The data presented here do not allow an assessment of predation risk. Predators, (snakes, birds, spiny lizards) may play a role in U. ornatus distribution. Circumstantial evidence suggests that predation risk may differ between the two habitats. Vitt et al. (1981) point out that the preferred habitat of U. ornatus always consisted of large mesquite trees forming a dense continuous canopy. This was confirmed in the present study (pers. obs., Russel 1985). The trees of the wash were larger and closer than trees of the flatland plot (Russel 1985). Urosaurus ornatus travel among trees. With a continuous canopy they can avoid ground travel and the inherent risks posed by ground dwelling predators. In addition, larger mesquite trees tend to have more crevices and loose bark, which the animals use for hibernation, thermoregulation, and hiding sites. With such characteristics, the higher density of lizards in the wash may reflect lower predation than in the flatland.

Based on arthropod density territories occupied by the different sexes did not differ. Urosaurus ornatus territories were found not to differ in arthropod density from those trees that were not occupied. This
lack in difference between occupied and unoccupied trees suggests there may be other factors preventing U. ornatus from occupying those trees not used. It may be that U. ornatus populations have not saturated this site, or that arthropod density may not determine habitat quality for U. ornatus.

The 1985 arthropod collection revealed the same seasonal pattern that existed in 1984. However, arthropod density was significantly lower in 1985 and the increase from the dry to wet season was not as dramatic as in 1984. The greatest seasonal increase was approximately 1.5 fold. Arthropod food resources were probably less limiting in 1984. Dunham (1980) found growth rate of U. ornatus to be lower in years of lower food resource density. Therefore, based on arthropod resource density, 1984 may have been a better year for U. ornatus.

Urosaurus ornatus forage on the ground and on the larger branches and trunks of mesquite trees (pers. obs., Vitt et al. 1981). Arthropod density on trees was estimated because on the two study plots U. ornatus spent the majority of their time in trees. Therefore, this estimate may be more representative of food availability. The ground arthropod estimates were significantly higher than the tree estimates. The tree estimates may be considered as the lower bound of
arthropods available to the lizards. Because the arthropod estimate within the tree canopy yielded the same seasonal trend in resource abundance as the ground data, the use of tree estimates would be as reliable as that of ground estimates.
Arthropod Resources and Tree Lizard Territories

Introduction

Territorial behaviour has been documented for many organisms (Brown and Orias 1970, Emlen and Oring 1977, Davies and Houston 1981, Stamps 1983, Davis and Murie 1985). Maintenance of a territory is the defense of an area by an individual or group (Davies and Houston 1984) that insures acquisition of some limited resource. These resources may include food, mates, nest sites or oviposition sites, and predator safe refugia (Gill and Wolf 1975, Brooke 1979, Davies and Houston 1981, Stamps 1983, Hurly and Robertson 1984, 1985, Stamps and Tollestrup 1984, Wolf 1985, Keen and Reed 1985, Ostfeld et.al. 1985). The territory defended by an individual should offer some benefit that would not otherwise be acquired if the territory were not held (Davies and Houston 1981, Fox et.al. 1981 Rose 1982, Stamps 1983, Paton and Carpenter 1984, Ruby 1984, Stamps and Tollestrup 1984, Ostfeld et.al. 1985). The benefits received by territory owners should confer higher fitness than non-territory holders.

Resource levels on territories may vary, and the quality of territories occupied by different individuals should reflect this. Not only may
territories differ in quality but areas that are defended should be of better quality than those that are not. Territory size often changes as a consequence of different resource levels (Gill and Wolf 1975, Simon 1975, Kodric-Brown and Brown 1978, Davies and Houston 1981). As territory quality declines, an individual is predicted to increase its territory size (Gill and Wolf 1975, Kodric-Brown and Brown 1978, Davies and Houston 1981), thereby insuring an adequate level of resources. If territory quality increased, then an individual would be expected to decrease its territory size (Gill and Wolf 1975, Kodric-Brown and Brown 1978, Davies and Houston 1981), because the costs of defending a large rich area will exceed the additional benefits acquired. Territory quality is an important factor in determining the size of a territory defended.

I estimated territory quality for U. ornatus in a mesquite wash in Southeastern Arizona. Arthropod density on each territory was used as an indicator of territory quality. Territory size was expressed by obtaining the minimum linear distance travelled by each territorial lizard. Territory features were compared between the sexes and among the males.
Methods

In a riparian woodland habitat *U. ornatus* territories were mapped using mark-recapture census techniques. The plot encompassed approximately 0.1 ha and included 24 mesquite trees that had continuous canopy. The plot was parallel to the wash, two to three trees in width. Three trees most distant from the wash did not have continuous canopies with the others.

During July and August 1985, *Urosaurus ornatus* were located and observed for 30 to 120 minutes without disturbance and their positions on the trees were recorded. Individuals that were not previously marked were captured by hand or with nooses, after the observation period and registered as described earlier (chapter 1). Positions of lizards on trees were marked with a permanent metal tag at the furthest point of travel on each branch. Positions were tagged only after observations had been terminated. On each occasion lizards were observed their positions were recorded. Territory size was estimated using the linear distance each lizard travelled by measuring the distance between the tagged positions at which each lizard was sighted. The total linear distance was used as an estimate of a tree lizard's minimum territory.
size. The relationship between male territory size and the density of arthropods (arthropods dm\(^{-2}\)day\(^{-1}\)) was investigated.

Lizard sightings occurred with different frequencies among the tree canopies. Sighting frequency may represent different levels of lizard activity. The different frequencies of lizard activity were hypothesized to represent locations of foraging preference. In order to test the hypothesis that tree lizard activity is determined by resource density, the arthropod density was measured at sites for which different frequencies of lizard activity within the tree canopy were present. Tanglefoot\(^\text{TM}\) cards were placed in different areas of lizard activity. The number of lizard records within a 1 m radius of the card were counted. Arthropod density was compared at different frequencies of \textit{U. ornatus} activity in the two seasons among the different lizard territories using a two-factor ANOVA.

Tree size was determined by measuring the branch circumference at each tagged position, and by recording branch and trunk circumference 1 m above the ground. Circumferences were converted to cross-sectional area (cm\(^2\)).
Results

Territory mapping provided 717 observations of 35 *U. ornatus* individuals, 17 males, 18 females. Mean male and female residency times (mean number of days present on study plot) of $12.67 \pm 3.69$ and $14.7 \pm 4.10$ days, respectively, did not differ ($t=0.3685$, df=20, $p > 0.50$). Males used significantly more mesquite trees ($\bar{x} = 2.71 \pm .51$) than the females ($\bar{x} = 1.33 \pm .19$) within their territorial boundaries (Kruskal-Wallis, df=1, $H=6.5297$, $p < 0.025$). Not surprisingly, since males used more trees, males had a significantly greater average linear distance ($36.4 \pm 11.23$) compared to the females ($8.7 \pm 1.75$, Kruskal-Wallis, df=1, $H=5.0987$, $p < 0.025$).

Arthropod density was compared between the male and female territories to determine if the sexes differed in the level of food resources available to them. The comparison revealed that the mean number of arthropods $dm^{-2}day^{-1}$ available to the males was not significantly different from that available to the females ($F = 0.005$, $p > 0.75$, Table 9, figure 8).

Inspection of the relationship between male territory size and the number of arthropods $m^{-1}$ of territory indicates a nonsignificant negative correlation; $r = -0.3622$, df = 9, $p = 0.602$ (figure 9).
Table 9: One-Way ANOVA of arthropod density (arthropods dm^{-2} day^{-1}) between the male and female territories, 1985.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among Groups</td>
<td>1</td>
<td>0.008</td>
<td>0.005</td>
<td>&gt; 0.75</td>
</tr>
<tr>
<td>Within Groups</td>
<td>163</td>
<td>250.334</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>164</td>
<td>250.342</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 8: Mean (+ 1 S.E.) arthropod density (arthropods dm$^{-2}$ day$^{-1}$) on male and female territories, 1985.
Figure 9: Log x log plot of the linear regression of arthropod density (arthropods dm$^{-2}$d$^{-1}$) on territory size.
$y = 48.75 - 0.359(x)$

$r = 0.337$
Therefore, territory size was independent of resources. The negative trend was expected based on the theory that individuals should alter territory size to maintain a constant level of resources.

The results of the comparison between the different levels of lizard activity and arthropod density indicated that there was no significant difference in arthropod food resources at the different frequencies of lizard activity (\( F = 1.36, p > 0.10 \), Table 10, figure 10). Lizards did not appear to frequent a particular locality within their territory based on food resource density.
Table 10 Two-Factor ANOVA of arthropod density (arthropods dm$^{-2}$day$^{-1}$) at different frequencies of lizard activity on territories, 1985.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>1</td>
<td>35.006</td>
<td>17.888</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Activity level</td>
<td>5</td>
<td>13.304</td>
<td>2.661</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>Interaction</td>
<td>5</td>
<td>8.16</td>
<td>1.632</td>
<td>&gt; 0.75</td>
</tr>
<tr>
<td>Error</td>
<td>123</td>
<td>240.724</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>134</td>
<td>297.194</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 10: Mean (± 1 S.E.) arthropod density (arthropods dm⁻² day⁻¹) at different frequencies of lizard activity during the dry and wet season.
Discussion

There are several different methods of estimating territory size, and all have unique problems (Jennrich and Turner 1969, Rose 1982). Rose (1982) reviewed the methods of determining home range and territory size estimates in lizards and found that the same data could result in different estimates when analysed by different methods. The reliability depends not only on the technique used but also on the accuracy with which sightings and measurements are obtained. The time interval over which home ranges or territories are measured may affect the estimates of territory size (Rose 1982). More sightings per animal or shorter time intervals between censuses will increase the accuracy of the estimate of territory size. While studying Sceloporus virgatus, Rose (1982) found that a minimum of eighteen sightings per animal were necessary to accurately measure home range size. This minimum sighting requirement was attained or exceeded for each individual used in my analysis. Because observations on lizards were continuous, problems with the census interval were reduced, thereby increasing the reliability of my territory size estimates.

The linear distance method employed here is a direct estimate of the minimum distance spanning an
individual's territory. Therefore, it is a conservative estimate of territory size. Data indicate that males occupy twice as many trees and traverse more than a 4-fold greater distance than females. The energetic requirements of the sexes are probably close to being equal, so the larger male territory must offer some benefit other than food acquisition. Females may not be able to afford the cost of defending a large territory because a larger amount of energy must be allocated to egg production. Males can allocate more energy to the defense of territories with the potential to maintain more than one female. In lizards and many other vertebrates, investigators have found that males tend to occupy territories twice as large as females and that female territories are maintained within those of males (Kodric-Brown and Brown 1978, Wolf 1980, Davies and Houston 1981, Ruby 1981, Hurly and Robertson 1984, 1985, Smith 1985). By defending larger territories, males may have exclusive access to two or more females, which may have significant implications for the organism's mating system (Emlen and Oring 1970). Evidence presented here suggests that females tend not to move great distances. Males on the other hand were observed to travel among trees, perhaps in search of females. Males travelling among trees potentially increase their encounter rate with females.
Urosaurus ornatus have been reported as having both a monogamous and polygynous mating system (Milstead 1970, Dunham 1982). Evidence reported here may be indicative of a polygynous mating system, but detailed female distributional data were not obtained to answer this question.

The quality of male and female territories, based on arthropod density, did not differ. This is consistent with the notion that larger male territories may indeed serve functions other than food acquisition. Individuals are expected to frequent better quality patches more often than poor patches. Therefore, different frequencies of lizard activity should reflect a difference in arthropod density at different locations within the tree. The frequency of lizard activity within the tree canopy did not depend on arthropod density.

Males defending large territories did not have a significantly higher density of arthropods than males with smaller territories. Male territory quality was independent of territory size. If territory size changes to maintain a constant level of food resources then a negative relationship between territory size and food abundance is expected. Simon (1975) conducted food supplementation experiments with Sceloporus jarrovi that provided evidence to support this
prediction. Natural food abundance was negatively correlated with territory size. When food was added territory sizes became significantly reduced. Although *U. ornatus* territory size and arthropods were negatively related it was not significant. Males that maintain a larger territory must be defending some resource other than food. These results suggest that the availability of arthropods may not be a major determinant of habitat choice by *U. ornatus*, which was the same conclusion reached from the 1984 data. When resources were significantly lower in certain years, resource abundance was a major factor in affecting life history parameters of *U. ornatus* (Dunham 1980). Though I have no assessment of such parameters in both years of the study, the data presented here suggest that arthropods are not a major factor.

With no consistent variation in arthropod density the function of territoriality must be determined by other resources. In an experimental manipulation of the sex ratio, M'Closkey et al. (unpublished manuscript) showed the function of territoriality differed between sexes of tree lizards. Females were found to be an important resource for males. Males defended territories for mating opportunities, whereas females may occupy areas where oviposition is safe.
Territory Defense in Tree Lizards

Introduction

Individual gains from territory defense may not be immediately realized. Individuals may derive either short- or long-term benefits in territory defense. This implies that an individual defending a territory is able to assess the profitability of available resources for immediate use, or realize the potential for future procurement of a crucial resource (Davies and Houston 1981, Stamps and Tollestrup 1984). Males will defend territories in anticipation of future mating opportunities (Emlen and Oring 1977, Davis and Murie 1985, Keen and Reed 1985, Ostfeld et.al. 1985, Smith 1985, Wickman 1985). Therefore, male defense of a territory is expected to cease when the prospect of future mating opportunities no longer exist. If male territorial behaviour is closely linked to mating success, then the defense of the territory should be influenced by reproductive activity.

The female U. ornatus reproductive cycle varies with geographic location. Females may be reproductively receptive at 4 different times in a season (Asplund and Lowe 1964, Martin 1973, 1977, Michel 1976, Tinkle and Dunham 1983). Male testicular
activity peaks from late April through September, with variation due to geographic location (Asplund and Lowe 1964, Martin 1973, 1977, Michel 1976, Tinkle and Dunham 1983). Males remain reproductively active for the entire season but there is a large reduction in testis size and spermiogenesis in late August (Asplund and Lowe 1964). Aggression in most iguanids corresponds with the breeding season and lower levels of testosterone at the end of the season should have the effect of reducing territorial defense (Fox et al. 1983). Male intraspecific territorial aggression should commence when the testicular cycle begins and terminate when the cycle ends.

With this difference in the reproductive biology of the sexes, there is an abrupt change in the operational sex ratio (number of reproductively receptive females / number of reproductively active males). With males being reproductively active for the entire season, the operational sex ratio is 1:1 or greater in the early spring and again in mid July when females are receptive i.e.: not gravid, but zero for the remainder of the season i.e.: no receptive females. Therefore, once mating has occurred in July there are no further opportunities for mating until the following spring. Access to mates, a major function of territoriality, no longer exists. For this reason a
reduction in territorial defense is expected, leading to a reduction in aggression and perhaps the breakdown of territory structure.

Success in territory defense has been associated with body size. Larger individuals are usually the most successful in capturing, defending, and holding a territory (Davis and Murie 1985, Christian and Waldshmidt 1984, Fox et al. 1981, Grossman 1980, Simon 1975, Licht 1974). Regardless of current territory ownership, larger lizards may be able to capture and defend a territory (Stamps 1978).

I experimentally introduced non-resident lizards into established territories to assess the behavior of resident territorial male U. ornatus. The following two hypotheses were tested: 1) Territorial behavior ceases when the prospects for future mating opportunities do not exist. 2) Successful defense of a territory depends on body size.
Methods

Male territory locations were determined from census data collected during May and June, 1985. The operational sex ratios (number of receptive females / number of sexually active males) were determined from the census data. Experimental introductions were conducted for seven days in July (n = 13 trials) and six days in August (n = 17 trials).

Prior to each trial, two male *U. ornatus*, previously marked and with known territories, were located. By random assignment, one individual was designated as intruder (non-resident) and the other as resident. The intruder was captured by hand or noose and taken from its territory and introduced into the resident's territory. The intruder was placed within 1 m of the resident. Response of the resident was of particular interest so its behaviour was monitored until the eviction of the intruder. Subsequent to the completion of the trial, both lizards were removed from the tree and the intruder was returned to the point of capture on its territory and given time (5 to 10 min) to settle before the reciprocal trial was conducted on its territory. The resident lizard of the first trial was left on its territory or held until the intruder was settled. The designated roles of the lizards in the reciprocal trial were the reverse of those in the first
trial. The resident of the first trial was designated as the intruder, and the original intruder was designated as the resident, now on its own territory.

Each trial was timed with a digital stopwatch and recognition of the intruder by the resident designated the start of the trial. Resident male response to an intruder was of particular interest, and for the resident, display frequency, attack frequency, and eviction time were recorded. Displays were recorded as of two types. Those designated as a "general display" consisted of a presentation by the male in which several "push ups" occur in rapid sequence. This was frequently observed as territorial males moved within their territories. This advertises ownership as a male patrols his territory. The second display is directed toward an intruding conspecific designated as "displays to intruders", which was the aggressive side-step approach and animated display toward an intruder (Carpenter 1983). The territory owner will approach the intruder and present himself sideways while doing "push ups". This display toward an intruder usually preceded an attack by the resident. These two display types were easily distinguished for male U. ornatus as indicative of aggression and territorial behaviour. The frequency of each display type was recorded and their frequency compared in a three-way ANOVA in the
presence and absence of females during July and August to test the aggression hypothesis. Females were considered present if sighted within the resident's territory during the trial; otherwise they were absent. The hypothesis predicts that territorial display frequency should decrease if aggression is decreasing. Display frequencies were transformed (Box-Cox, lambda = 0, Sokal and Rohlf 1981). Males were also observed performing courtship displays.

The attack frequency was recorded as the frequency of aggressive encounters during the length of time the intruder remained on the resident's tree. Attacks were recorded for both residents and intruders which involved one lizard chasing and usually biting the other. Attacks were invariably initiated by the resident. Attack frequencies on the intruder by the resident were monitored and compared between the two months in the presence and absence of females. The hypothesis predicts that attack frequency should also decrease if aggression is decreasing. Attack frequencies were transformed (Box-Cox, lambda = 0, Sokal and Rohlf 1981). The attacks usually led to immediate eviction of the intruder.

The eviction time was recorded as the time elapsed between the discovery of the intruder and the eviction of either lizard from the tree. The trial was
terminated by eviction of either the intruder or the resident from the tree. The intruder eviction times were compared between the two trial periods in the presence and absence of females using a two-factor ANOVA. It was predicted that in August residents should be more tolerant of an intruder's presence and take longer to evict it.

The body size (SVL) of winners and losers (evicted) were compared using Wilcoxon’s signed-ranks test (Sokal and Rohlf 1981), to determine the significance of body size on the outcome of territory contests.

Results

Female U. ornatus are reproductively receptive in mid-May and again in mid-July. At my study site two clutches per year were observed (early July and late August), and oviposition by all females took place within a 4 to 5 day period in early July signifying a highly synchronized reproductive cycle. By late July all females were gravid a second time and oviposition occurred in late August. Males were reproductively active by mid April and remained so until late August.

Display frequency was significantly higher during the July than during the August trials (F = 6.238, p <
Table 11: Means and standard errors of display frequencies between months with females present and absent (sample sizes in brackets). The Three-Factor ANOVA uses the Box-Cox transformation. A is the month effect, B is the display effect (display type) and C is the female presence effect.
<table>
<thead>
<tr>
<th>Month</th>
<th>Female Presence</th>
<th>Display Toward Intruder/min</th>
<th>General Display/min</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>July</td>
<td></td>
<td>0.7573 ± 0.2655 (11)</td>
<td>0.1527 ± 0.0574 (11)</td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td>5.28 ± 4.32 (2)</td>
<td>0.255 ± 0.255 (2)</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Present</td>
<td>0.432 ± 0.1327 (10)</td>
<td>0.162 ± 0.0492 (10)</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td>0.4729 ± 0.1264 (7)</td>
<td>0.1243 ± 0.0356 (7)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (season)</td>
<td>1</td>
<td>6.606</td>
<td>6.238</td>
<td>&lt; 0.025</td>
</tr>
<tr>
<td>B (displays)</td>
<td>1</td>
<td>1.359</td>
<td>1.284</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>C female presence</td>
<td>1</td>
<td>0.309</td>
<td>0.292</td>
<td>&gt; 0.50</td>
</tr>
<tr>
<td>AB</td>
<td>1</td>
<td>0.392</td>
<td>0.369</td>
<td>&gt; 0.50</td>
</tr>
<tr>
<td>AC</td>
<td>1</td>
<td>1.477</td>
<td>1.394</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>BC</td>
<td>1</td>
<td>1.200</td>
<td>1.133</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>ABC</td>
<td>1</td>
<td>0.196</td>
<td>0.185</td>
<td>&gt; 0.50</td>
</tr>
<tr>
<td>Error</td>
<td>52</td>
<td>55.074</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>59</td>
<td>59.732</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
0.025, Table 11). The two display types did not differ in frequency (F = 1.284, p > 0.25, Table 11), nor did display frequency differ in the presence and absence of females (F = 0.292, p > 0.50, Table 11). These data provide some support for the hypothesis. Display frequencies decreased near the end of the breeding season, suggesting that aggression decreased.

The attack frequency between the two months and in the presence or absence of females did not differ (Table 12). Therefore, there was no reduction in attack frequency from July to August. Therefore, no evidence for a decrease in aggressive behaviour: There was a tendency for attack frequency to be lower in August, (as the hypothesis predicts, figure 11).

There was no significant difference in eviction times between the two months (F = 0.857, p > 0.25, Table 13) even though eviction time was longer in August (figure 12). There is also no significant difference due to female presence or absence (F = 0.565, p > 0.10, Table 13). Intruders were not evicted faster when there was a female present on the resident's territory. These results indicate no significant increase in eviction time from July to August, suggesting no decrease in intraspecific territorial aggression.

Body size in both July and August was not significant in determining the outcome of the trials (
Table 12: Two-Factor ANOVA of attack frequencies using transformed data (Box-Cox, $\lambda = 0$), between July and August in the presence and absence of females.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Month</td>
<td>1</td>
<td>0.011</td>
<td>0.009</td>
<td>&gt; 0.75</td>
</tr>
<tr>
<td>Female effect</td>
<td>1</td>
<td>0.5069</td>
<td>0.433</td>
<td>&gt; 0.50</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>1.6341</td>
<td>1.395</td>
<td>&gt; 0.10</td>
</tr>
<tr>
<td>Error</td>
<td>26</td>
<td>30.4621</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>32.6141</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 11: Mean (+ 1 S.E.) attack frequency by residents on intruders during July and August in the presence and absence of females.
Table 13: Two-Factor ANOVA of intruder eviction times (seconds) during July and August in the presence and absence of females.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Month</td>
<td>1</td>
<td>1270800</td>
<td>0.8571</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>Female presence</td>
<td>1</td>
<td>836954</td>
<td>0.5645</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>1053940</td>
<td>0.711</td>
<td>&gt; 0.25</td>
</tr>
<tr>
<td>Error</td>
<td>26</td>
<td>38549400</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>41711100</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 12: Mean (± 1 S.E.) Intruder eviction time during July and August in the presence and absence of females.
July: $T = 26.5$, $p > 0.05$, August: $T = 60.0$, $p > 0.05$, Table 14). Of 30 trials conducted, resident lizards evicted the intruder 29 times. In every trial the resident was the aggressor in any confrontation that occurred. One trial was not completed due to lizard inactivity during intense heat. The change in behaviour from winning as a resident to losing as an intruder, irrespective of body size, was significant by McNemar's test (Table 15). The outcome of these trials suggests that body size is not an important determinant in territory defense of U. ornatus, giving no support for the body size hypothesis.
Table 14: Comparison of lizard body sizes of introduction trials using Wilcoxon's signed-ranks test, 1985.

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
<th>Combined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Trials (n)</td>
<td>13 (11)</td>
<td>17</td>
<td>28</td>
</tr>
<tr>
<td>Frequency of Winner Larger</td>
<td>3</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Frequency of Loser Larger</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Frequency Loser = Winner</td>
<td>5</td>
<td>11</td>
<td>16</td>
</tr>
<tr>
<td>Wilcoxin Statistic (T)</td>
<td>26.5</td>
<td>60.0</td>
<td>164.0</td>
</tr>
<tr>
<td>p</td>
<td>&gt; 0.05</td>
<td>&gt; 0.05</td>
<td>&gt; 0.05</td>
</tr>
</tbody>
</table>
Table 15: McNemar Test for a change in behaviour of *Urosaurus ornatus* during the introduction trials, 1985.

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
<th>Combined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Trials</td>
<td>12</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>Resident Stay</td>
<td>12</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>Resident Left</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Intruder Stay</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Intruder Left</td>
<td>12</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>G Statistic</td>
<td>16.636</td>
<td>13.863</td>
<td>30.499</td>
</tr>
<tr>
<td>p value</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Discussion

Three lines of evidence were used to assess the territorial aggression of male tree lizards toward male conspecific intruders. Previous work showed that males do not defend territories on the basis of food abundance (Chapter 1 and 2) but rather on the defense of mates (M'Closkey et al. unpublished). Mate defense has been proposed as a function of territoriality (Emlen and Oring 1977, Grossman 1980, Ruby 1984, Hurly and Robertson 1984, 1985, Davis and Murie 1985, Keen and Reed 1985, Smith 1985, Wickman 1985), but territoriality may have other functions such as food acquisition, predator refuges, and oviposition sites (Milstead 1970, Gill and Wolf 1975, Simon 1975, Davies and Houston 1981, Stamps 1983, Paton and Carpenter 1984, Andrews 1985, Hurly and Robertson 1985, Ostfeld 1985). Territory function may change over time (Stamps 1983, Davis and Murie 1985) or may serve concurrent functions (Ruby 1981, Andrews 1985).

_**Urosaurus ornatus** is a member of the family Iguanidae, and like other members of the family, has characteristic territorial displays. Display behaviour differs among the family members (Carpenter 1967, 1983), but 3 major roles have been identified: 1) advertising related to mating behaviour, 2) advertising
for territory ownership and 3) advertising social dominance.

As expressions of aggression and territorial behaviour, the testicular aggression hypothesis implies that the frequency with which these displays occur should be positively associated with testosterone levels. Increase in testosterone levels has been shown to be positively correlated with male aggression and territorial tendencies in other species (Fox 1983, Davis and Ford 1983, Moore 1984). As males emerge from hibernacula, the increase in testosterone levels enhances territorial behaviour. As long as testosterone levels remain elevated, intraspecific territorial aggression should occur. Testosterone levels in *Urosaurus ornatus* reach high levels soon after emergence from hibernacula and do not decline until August (Asplund and Lowe 1964). Therefore, aggression is expected to decline late in the season. Davis and Ford (1980) found *Sceloporus occidentalis* defense of home range was associated with the period of increased levels of testicular activity and concluded that females were the primary resource being defended. Experimental evidence reported here using display frequency as one measure of aggression, supports this testicular aggression hypothesis. As the breeding season terminates, display frequencies decline
indicating that aggression is declining and female defense may cease to be a priority.

Like display frequencies, attack frequencies should decline for the same reasons. Attacks on an intruder clearly indicate active aggressive behaviour exhibited by the resident. Obviously, the resident will not tolerate the intruder on his territory since the resident was observed to persist in its offensive behaviour until the intruder was evicted. Attack frequency tended to be lower in August, but the analysis indicated that attack frequency did not decrease as predicted. This result fails to support the aggression hypothesis.

In a different taxonomic group (Pisces: Gobiedae) resident bay gobies successfully evicted intruders from mud flats more often than intruders evicted residents (Grossman 1980). However, individuals that won a previous bout and those that initiated the bout had a greater chance of winning the next bout. Resident _U. ornatus_ always won a trial but when a resident's role was changed to that of intruder, unlike the bay goby, it never won. Previous ownership is the determining factor in success of holding a territory for _U. ornatus_.

If aggression were to decline as predicted, then residents should become more tolerant of intruders late
in the season. Residents should not be so quick to evict intruders, and eviction times are expected to increase. However, the experimental introductions falsify this hypothesis. Eviction times do not differ between July and August. This indicates that aggression did not subside. Aggression in *Sceloporus virgatus* was restricted to the breeding season (Smith 1985), suggesting that defense of territories is related to mate defense. With this continued territory defense in male *U. ornatus*, one possible function of territorial defense, female defense, may remain important, or perhaps until the second clutch is oviposited, or some other factor is responsible for the continued defense.

In addition, the effect of female presence was not significant. If males are defending females then residents should be more aggressive toward intruders when females are present. Smith (1985) found male *Sceloporus virgatus* to interact with more intensity in the presence of females than in their absence. This was not the case for male *U. ornatus*. Male *U. ornatus* were observed to travel the length of their territory, court a female when encountered, and continue surveying the territory. Therefore, when a resident male encountered an intruder he may behave as if a female were present. In addition, with catchabilities of
approximately 50% (pers. obs., Russell 1985) females may have been present but missed during a particular census. This may explain the lack of the female presence or absence effect in the trials.

Overall, there is little evidence for a reduction in territory defense by resident male *U. ornatus* between July and August. A reduction was expected to coincide with the decline in the operational sex ratio and spermiogenisis after mid-July. Although there was a reduction in the frequency of displays by resident males between July and August, there was no significant change in attack frequency or eviction time of an intruder. Though display frequency may indicate a reduction in aggression, display frequency may only represent passive aggression whereas attack frequency and eviction of an intruder is active aggressive behaviour. These results indicate that territories can not be invaded by conspecifics. Davies (1975) observed that territories of pied wagtails could be invaded under certain circumstances by subordinate conspecifics. The territory of male *U. ornatus* may continue to serve some special function, such as providing overwintering sites, predation refuges, or increased hatchling survivorship and these may provide the stimulus for continued defense.

Body size has been implicated in successful defense

A higher rate of success could be reflected in higher feeding rates (Kodric-Brown and Brown 1978, Davies and Houston 1984), access to predator-safe sites (Stamps 1983), and more mating opportunities (Emlen and Oring 1977, Wickman 1985). Individuals lacking territories may not acquire the same level of resource, and may suffer higher mortality rates than territorial individuals.

Body size of U. ornatus was not important in determining the trial outcome. In another iguanid lizard, Sceloporus virgatus, 74% of pairwise encounters were won by larger males although median snout-vent lengths differed by only 2.2 mm (Smith 1985). Those males that won were able to mate, thus body size played an important role in mating success. There was no evidence of a dominance hierarchy among U. ornatus. In every trial, the lizard designated as the resident won an encounter, evicting the intruder irrespective of
body size. Of those lizards involved in reciprocal trials, residents always won. Of eight trials that were not reciprocal, the same pattern occurred. There was no evidence found to support the body size hypothesis. Body size may be a significant factor in early territory contests (April-May). However, once territories are established, the simple "resident wins" rule prevails.
Assessment of Competitive Interactions

Introduction

Despite a rich literature on lizard ecology (Huey et al. 1983), very few investigators have studied interspecific competitive interactions for sufficient time to detect its frequency of occurrence and mode of action (Dunham 1980, Smith 1981, Tinkle 1982). One conclusion of long-term investigations is that competition may be either absent or transient, expressed only under conditions of severe resource limitation. By their nature, short-term studies usually cannot reveal either variation in the intensity of competition or possible effects of competition on fitness (but see Pacala and Roughgarden 1982). However, individuals do respond to manipulations of food or conspecific density (Simon 1975, Ferguson et al. 1983, Fox 1983). Such manipulations often produce immediate adjustments in behaviour and the use of space. Therefore, short-term investigations are useful as preliminary studies to design long-term manipulations and predict the outcome of a specific interaction.

In a study on factors affecting tree lizard (Iguanidae, Urosaurus ornatus) numbers, a peculiar distributional relationship between U. ornatus and
spiny lizards (Iguanidae, *Sceloporus magister*) was observed (pers. obs.). At the Rincon Unit of the Saguaro National Monument, Southeastern Arizona, *S. magister* adults are common in flatland desert habitat dissected by mesquite (*Prosopis juliflora*) - catclaw (*Acacia greggii*) riparian woodland. However, adult spiny lizards are rarely seen in the riparian habitat. Yearling spiny lizards are common in the washes, and some of the mesquite trees are occupied by both resident tree lizards and yearling spiny lizards. This investigation of lizard distribution was designed to detect any effects *Sceloporus* spp. imposed on *Urosaurus ornatus* growth, feeding rates, and residency. Trials were conducted during the dry season (March-June, 1984) when lizard numbers and individual growth rates are high, territories are established, and arthropod abundance is relatively low. Therefore, any interactions that may occur should be expressed or amplified during the dry season.

Methods

Six dry season censuses of tree lizards at the Saguaro National Monument, Arizona, were conducted from March-June, 1984. The study plot (Wash 0.22 ha) was a mesquite-acacia riparian woodland containing 51 trees.
Captured lizards were marked, weighed measured (snout-vent length), and released. Only the snout-vent lengths were used for analysis of growth rates (Smith 1981). Each tree on the study plot served as a census unit. Lizard territories consisted of one to three trees, and each tree could be classified as either containing resident lizards or having no residents. To analyze the joint distribution *U. ornatus* and *S. magister* a 2 x 2 table of presence and absence frequencies was constructed. The resident category indicates that a lizard was present during at least two (not necessarily consecutive) censuses. However, all spiny lizards were resident during the entire dry season, at the time of maximum individual growth and territory establishment of the tree lizards.

Growth rates of tree lizards were analyzed by the methods of Pacala and Roughgarden (1982). Neither the initial nor the final snout-vent lengths of the two groups of *U. ornatus* (presence and absence of spiny lizards) differed. Therefore, the growth rate (mm d⁻¹) distributions of the two groups were compared, keeping the sexes separate.

A series of trials were conducted to examine any behavioural effect of spiny lizards on *U. ornatus*. Time constraints and low numbers of spiny lizards did not permit an evaluation of any reciprocal effects. Spiny
lizards (12-34 g) were much larger than *U. ornatus* (4-5 g), so asymmetry in any interactions that might occur was expected. Because spiny lizards and *U. ornatus* were observed on large mesquite branches in the riparian habitat, an enclosed branch was used as the experimental unit. A 1 m section of mesquite branch was enclosed with two discs of hardware cloth (10 cm diameter) attached perpendicular to the branch. Aluminum sheet was riveted to the hardware cloth forming an outer disc 30 cm wide (figure 13). This arrangement allowed small arthropods free access to the branch enclosure, allowed the lizards to see the surrounding area outside the enclosure, and prevented lizards from escaping the enclosure unless they jumped from the branch, which they did infrequently.

The basic question of interest was, does *U. ornatus* retreat from branches on mesquite trees when they encounter larger spiny lizards? For each trial with the spiny lizard present, the two lizards were placed opposite one another approximately 2 dm apart on the surface of the branch. Retreat was indicated by *U. ornatus* either attempting to climb the hardware cloth screen or jumping from the branch. The elapsed time for either type of retreat to occur was recorded. The spiny lizards in all of our trials were quite content to sit on the enclosed branches. The trials were
Figure 13: Diagram of enclosure used for interaction trials between *U. ornatus* and *Sceloporus* spp.
designed as a paired control and treatment. For controls a tree lizard was placed in the enclosure alone whereas treatments included the simultaneous introduction of a tree lizard and spiny lizard. To control for highly individualized U. ornatus behaviour the order of control and treatment for each lizard was randomized and the trials analyzed by Wilcoxon's signed ranks test. Lizards were allowed to settle for 1 min before observations on their interactions and time to departure from the branch enclosure was recorded.

In all, 100 trials were conducted and divided into eight sets (n=9-14). Six different spiny lizards were used: one male and three female S. magister, and two male S. clarki, another spiny lizard species occasionally found as yearlings in riparian habitat. No sexual dimorphism is evident among yearlings of either Sceloporus spp, and no differences in male and female behaviour were noted in the branch enclosures. The trials were conducted in June and July. In two sets of trials (n=18) female U. ornatus were used. During the period when females were obviously gravid (late June) only male U. ornatus (n=82) were used.

Another branch enclosure was used to examine whether spiny lizards depressed the feeding rate of tree lizards. In a single series of trials (n=14) the abundance of ants was increased on the enclosed branch
by dabbing a mixture of peanut butter, ground meat, and flour onto the sides of the branch. Although ant counts were not taken, this procedure always insured several columns of ants along the branch. If the ants were not continually present, the trials were stopped. The number of ants eaten in 10 min trials was recorded. Each *U. ornatus* was used as a control (alone) and treatment (*S. magister* yearling present), with the order randomized to avoid satiation and experience biases. Lizards were returned to their sites of origin after the completion of trials. Any lizards requiring overnight maintenance were housed in 100 l aquaria with rocks and gravel and ants (for *U. ornatus*) or grasshoppers (for spiny lizards). Lizards were allowed to warm-up in aquaria in the field prior to testing. Behavioural thermoregulation was regularly observed.

**Results**

From March 29 to June 28, 1984, 136 *U. ornatus* were marked on 51 mesquite trees in the riparian habitat. During this period six censuses produced 263 total captures. *Urosaurus ornatus* numbers declined from 1.05 lizards tree\(^{-1}\) census\(^{-1}\) in March to 0.53 lizards in late June. Of the total number of *U. ornatus* marked, 92 established residence on the plot.
(captured during two or more, not necessarily consecutive, censuses), of which 41 were male and 51 female. During the same period the presence of 13 resident yearling *S. magister* were noted. Early in the dry season it was possible to mark some of these individuals, but later visual sightings were relied upon to confirm residence by a spiny lizard. Only two *SceIoporus clarki* juveniles were noted during the census.

To evaluate the independence of the distribution of tree and yearling spiny lizards, the presence or absence of resident lizards were tallied. Each mesquite tree constituted one spatial sampling unit, and the results show a significant departure from independence of occurrence (table 16). However, the direction of the departure was a positive association between the species. Both appeared to be responding to the same general features of the riparian trees and occupied trees together more frequently than expected by chance. Tree size or a covariate may be important in determining where lizards establish residence. Both lizards occupied trees that are significantly larger than those trees not occupied by resident lizards (M'Closkey, unpublished data). There were insufficient *S. clarki* sightings to examine their spatial
Table 16: Observed and expected (in parentheses) frequencies of trees containing resident lizards. The null hypothesis of independent distributions is rejected (G = 10.54, p < 0.005) in the direction of positive association of the species.

<table>
<thead>
<tr>
<th></th>
<th>S. magister</th>
<th>Absent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td></td>
<td>11 (6.1)</td>
<td>13 (17.9)</td>
</tr>
<tr>
<td></td>
<td>U. ornatus</td>
<td>Absent</td>
</tr>
<tr>
<td></td>
<td>2 (6.9)</td>
<td>25 (20.1)</td>
</tr>
</tbody>
</table>
relationship with *U. ornatus*.

The dry season growth rates of resident *U. ornatus* classified as either co-occurring with *S. magister* or living alone were examined. The growth rate (mm d\(^{-1}\)) was regressed against initial snout-vent length (Fig. 14). All slopes are significantly less than zero (males, *Sceloporus* present, p < 0.05; males, *Sceloporus* absent, p < 0.01; females, p < 0.001). For each sex, neither the initial (males, D=0.208; females, D=0.257) nor the final (males, D=0.167; females, D=0.121) snout-vent lengths differed in the presence or absence of spiny lizards (all p's > 0.1, Kolmogorov-Smirnov two sample test). Because the size distributions of *U. ornatus* did not differ as a result of spiny lizard residence, the growth rate distributions of *U. ornatus* was compared by pooling the individuals of each sex (Pacala and Roughgarden, 1982). Mean growth rates (mm d\(^{-1}\)) for male tree lizards in the presence and absence of spiny lizards were 0.08 ± 0.014 and 0.08 ± 0.018, respectively (D=0.167, p > 0.1). For female *U. ornatus* the growth rates in the presence and absence of spiny lizards were 0.13 ± 0.015 and 0.12 ± 0.020, respectively. The observed growth rates are within the ranges reported by Smith (1981) for *U. ornatus*.

All spiny lizards observed in mesquite trees were resident during the entire dry season, but *U. ornatus*
Figure 14: Growth rate (mm/d) - snout-vent length (mm) regressions for male and female tree lizards in the presence and absence of *S. magister* yearlings. All slopes are significantly less than zero.
MALE UROSAURUS

SCELOPORUS ABSENT
(n=12)

SCELOPORUS PRESENT
(n=15)

FEMALE UROSAURUS

SCELOPORUS ABSENT
(n=19)

SCELOPORUS PRESENT
(n=17)

RATE (mm/day)

GROWTH

SNOUT-VENT LENGTH (mm)
showed substantial variation in residency time. Although growth rates of *U. ornatus* were not reduced by spiny lizard presence, occupancy time of trees could be depressed. Male residency in the presence and absence of spiny lizards averaged $47 \pm 5.6$ and $41 \pm 4.4$ days, respectively. Female residency averaged $56 \pm 5.4$ and $48 \pm 5.7$ days in the presence and absence of spiny lizards, respectively. None of the variation in *U. ornatus* residency time was due to the presence of spiny lizards (males, $D=0.317$; females, $D=0.272$, $p > 0.1$).

The growth rate and residency data failed to reveal evidence of interactions on *U. ornatus* by spiny lizards; however, aggression between the lizards was examined. The mesquite trees occupied by both lizards were large enough so that direct encounters between the lizards could be infrequent. Nevertheless, *U. ornatus* were aware of the presence of spiny lizards and male *U. ornatus* (50-55 mm snout-vent length) frequently approached the larger spiny lizards (60 mm) and advertised their presence. Spiny lizards did not overtly respond to *U. ornatus*. The branch enclosure was designed to confine lizards and amplify the expression of any aggression. Table 17 summarizes the results of 100 trials, where the branch residence time of *U. ornatus* is the criterion variable. Mean branch times for the different trials ranged from 3 to 7 min.
Table 17: Mean branch enclosure time (min:sec) for tree lizards in the presence (treatment) and (absence) of spiny lizards. Differences for each of the eight sets of trials were evaluated by Wilcoxon's signed ranks test (T).

<table>
<thead>
<tr>
<th>Spiny lizard</th>
<th>Mean Branch Time</th>
<th>Wilcoxon</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. magister</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male, 30g, n=14</td>
<td>6:16</td>
<td>5:42</td>
</tr>
<tr>
<td>Female, 23g, n=14</td>
<td>4:42</td>
<td>6:35</td>
</tr>
<tr>
<td>Female, 12g, n=13</td>
<td>5:37</td>
<td>7:03</td>
</tr>
<tr>
<td>Female, 12g, n=9</td>
<td>4:23*</td>
<td>3:22*</td>
</tr>
<tr>
<td>Female, 12g, n=13</td>
<td>6:02</td>
<td>6:49*</td>
</tr>
<tr>
<td>Female, 12g, n=9</td>
<td>4:12*</td>
<td>6:26*</td>
</tr>
</tbody>
</table>

| S. clarki     |                  |          |
| Male, 18g, n=14 | 5:55             | 5:16     | 28 | NS |
| Male, 34g, n=14 | 4:06             | 6:49     | 23 | <.05 |

*Trials with female tree lizards. All other trials used males.
However, the data were not analyzed by comparing the means because of high variation in activity among _U. ornatus_. Instead, each set of trials was evaluated by Wilcoxon's signed ranks test. Clearly, there is no evidence to support the hypothesis of aggression by spiny lizards at the level of a single mesquite branch. In five of the eight trials, _U. ornatus_ spent more time in the branch enclosure in the presence than in the absence of spiny lizards. The single set of trials to show a significant effect (Table 17) involved _S. clarki_, an infrequent occupant of mesquite trees with tree lizards. The _S. clarki_ trials also falsified the hypothesis of interference because the direction of departure was opposite to the predicted effect: _U. ornatus_ spent more time on the branch enclosure with a spiny lizard than in its absence.

Finally, the feeding rate of _U. ornatus_ in the presence and absence of spiny lizards was examined by counting the ants eaten by _U. ornatus_ under control (alone) and treatment (with a spiny lizard) conditions. Although _U. ornatus_ ate more ants when alone, the difference was not significant (Table 18). In addition, the two highest feeding rates (19 and 22 ants eaten per 10 min) occurred in treatments involving spiny lizards. Therefore, the presence of spiny lizards does not appear to depress the feeding rate of
U. ornatus. The observed feeding rates were higher than those reported by Dunham (1980) on free-ranging tree lizards, suggesting that lizard behaviour was not adversely affected by the manipulations.
Table 18: Mean number of ants eaten by male tree lizards on a branch enclosure in the presence (treatment) and absence (control) of a yearling male *S. magister* (30 g, 80 mm snout-vent length). Difference was evaluated by Wilcoxon's signed ranks test (T).

<table>
<thead>
<tr>
<th>Tree lizards</th>
<th>( \bar{x} )</th>
<th>se</th>
<th>n</th>
<th>T</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>7.4</td>
<td>1.83</td>
<td>14</td>
<td>39</td>
<td>NS</td>
</tr>
<tr>
<td>Treatment</td>
<td>5.3</td>
<td>2.00</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Discussion

The investigations reveal no short-term competitive effects on U. ornatus by yearling spiny lizards. Urosaurus ornatus occurred with spiny lizards more frequently than expected. However, growth rates and residency of individual U. ornatus were not reduced in the presence of spiny lizards. Although it is not possible to say anything about resource limitation in the absolute sense, during the study period, resource levels (arthropod abundance) were approximately one-third the wet season (July-August) level. Urosaurus ornatus numbers declined during the wet season and, combined with the increase in food abundance, the effects of competition may be diminishingly small and difficult to detect. In addition, one could ask whether competition from single spiny lizards on trees, even under severe resource shortage, could produce a measurable depression of growth, residency, or feeding success of U. ornatus. Because both lizards occupy large riparian trees the frequency of contact between individuals may be very low.

Vitt et al. (1981) reported dense populations of U. ornatus and spiny lizard adults in riparian habitat. At their study site it appears that the potential for interactions between lizards would have been much greater than on my study area. Other reports
(Parker and Pianka 1973, Tinkle 1976) indicate frequent occurrence of S. magister adults in riparian habitats, hence my observations on age-specific habitat differences within S. magister appear unusual. Smith (1981) detected competitive interactions between tree lizards and another spiny lizard (S. virgatus). The potential for competition in Smith's system was also greater than that reported here. While his tree lizard numbers are slightly lower than mine S. virgatus was abundant and far more numerous than my S. magister yearlings. Tinkle (1982) reported no competition following a density manipulation involving three iguanid lizard species. However, Dunham (1980) detected a competitive effect on U. ornatus by S. merriami. In Dunham's study both lizard species had densities comparable to those of my tree lizards. Therefore, my study differs in an important way from the investigations cited above: the putative competitor (S. magister yearlings) occurred at low density with tree lizards.

Cumulative, long-term effects of competition cannot be ruled out. Smith's demonstration of competitive interactions applied only to young lizards, but more importantly, there was a time lag, with the competitive effect appearing in the year following the density manipulation. Competitive effects on that time
scale cannot be revealed by my studies. Based on the results of these short-term investigations long-term manipulations involving this pair of lizards would be feasible only if either of two conditions are fulfilled: (1) There is a substantial increase in the abundance of yearling spiny lizards in the riparian habitat in subsequent years; and (2) There is a reduction in dry season arthropod abundance in subsequent years providing the basis for relative resource limitation.
Summary

1. Habitat use by *Urosaurus ornatus* was studied in riparian and flatland desert habitats at the Saguaro National Monument, Rincon Mountain Unit, Arizona, during the spring and summer (March-August) 1984 and (May-August) 1985.

2. *Urosaurus ornatus* densities were higher on the riparian than the flatland plot.

3. Arthropod abundance varied seasonally. Arthropod abundance (arthropods dm\(^{-2}\)day\(^{-1}\)) increased 3.5-fold and 1.5-fold in the wet season during 1984 and 1985, respectively. Arthropod abundance did not differ between habitats. Arthropod abundance was significantly higher in 1984 than 1985 during both dry and wet seasons.

4. Territories of tree lizards did not differ in arthropod abundance. There was no difference in arthropod abundance between territories of different sexes or between occupied and unoccupied trees.

5. Tree lizard territory size was estimated and differed between sexes. Males defended territories four times larger than those of females. Individual male territories encompassed significantly more trees (\(\bar{x}=2.7\)) than did those of females (\(\bar{x}=1.3\)).

6. The frequency of lizard sightings in canopies of mesquite trees was independent of arthropod abundance.
7. Male intraspecific territorial aggression was assessed with intruder introduction trials. There was no overall indication of a decrease in aggression as the breeding season ended. Intruders were actively evicted in every trial. Display frequency decreased as expected but attack frequency and intruder eviction time did not decrease or increase, respectively, as predicted. Males were not more aggressive in the presence of females than in their absence.

8. Interactions between tree lizards and spiny lizards were assessed. There was a positive association in the distribution of the two species. Despite this association there was no reduction in growth rate or residency time of the tree lizards.

9. Tree lizard behaviour was assessed in the presence and absence of spiny lizards within experimental enclosures. The presence of spiny lizards had no affect on tree lizard residency time or feeding rate.
Conclusion

There was no evidence to suggest that *Urosaurus ornatus* distribution and territory defense were related to or dependent on arthropod density. Despite the significantly higher density of *U. ornatus* on the wash plot compared to that of the flatland, there was no difference in arthropod density and those trees occupied and defended by lizards did not differ in arthropod density from unoccupied trees. In addition, a non-significant negative relationship between territory size and arthropod density was found. These results suggest that *U. ornatus* may not be resource limited and *U. ornatus* distribution and territory defense are independent of arthropod density.

The continued defense of territories late in the reproductive season must be influenced by some factor other than food resources. Because there was no difference in aggressive behavior of males in the presence and absence of females, continued defense of a territory may insure successful oviposition. Therefore, the distribution of *U. ornatus* and the use of some trees and not others, may be closely linked to the success in which females can oviposit: locations with loose soil and appropriate amounts of debris and foliage cover allowing for successful oviposition may be preferred sites for territory defense. In addition,
some degree of habitat complexity may be necessary for predator avoidance. Males that defend habitats of preferred oviposition sites, predator safe sites and winter hibernacula should have more mates, higher hatchling survivorship, and perhaps higher overall fitness. Measurement of habitat structure and individual success will be necessary to further understand *U. ornatus* distribution.

In an investigation of the assessment of competitive effects of spiny lizards on *U. ornatus*, no short-term effects were detected. This does not rule out the possible importance of such competitive effects over a long time period. Detection of competitive effects such as reduced growth rates, lower survivorship, and an alteration in *U. ornatus* distribution may require an extensive long-term study involving removal experiments. The impact of other competitors and predators may have an important role in *U. ornatus* distribution.
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