

AGGRESSION AND THE DEVELOPMENT
OF TERRITORIALITY IN THE
DESERT SIDE-BLOTCHED
LIZARD,
UTA STANSBURIANA

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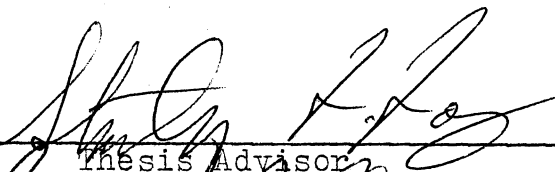
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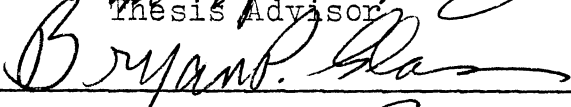
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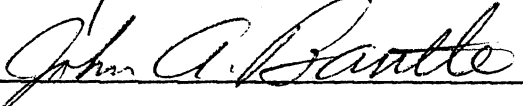


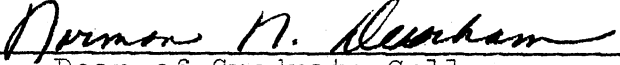
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Thesis Approved:



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PREFACE

This study concerned itself with the role aggression plays in home range acquisition in the juvenile Desert Side-blotched Lizard, Uta stansburiana. The primary objective was to determine the relationship between aggression and acquisition of a superior home range. Testosterone proprionate implantations were used to increase an individual's level of aggression. Another objective was to examine the effects of testosterone upon a juvenile's physiology and reproductive anatomy.

The author wishes to express gratitude to his major advisor, Dr. Stanley F. Fox, for his guidance, assistance, and support throughout this study. A note of appreciation is also given to the two committee members, Dr. John Bantle and Dr. Bryan P. Glass for their aid. Dr. Milton Curd greatly assisted in the histological assay. Thanks are also given to Charles Boydston, Charles and Judith Bloom, and Karen Fox for their valuable assistance collecting data during the field experiment. Texas Tech graciously consented to our use of their Field Station in Wink, Texas, while the University of Texas of the Permian Basin gave us free access to much of their laboratory equipment. Appreciation is extended to Ms. Catherine Schreiber for proofreading and critiquing the final manuscript as well as for her moral support. Ms. Sheila Garza did an

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CHAPTER I

THE RESEARCH PROBLEM

Introduction

Many vertebrates occupy individual areas more or less exclusively and exclude other conspecifics by some means of aggression. This is one definition of territoriality (Wilson, 1975). Territoriality is maintained through natural selection on an individual basis; the possession of a territory enhances individual fitness. Among lizards, as in many vertebrates, individuals with larger or otherwise superior territories survive longer or produce more progeny than those from inferior territories (Tinkle, 1969; Fox, 1973, 1978; Boag, 1973). Studies have also shown a correlation between level of aggression and acquisition of a superior territory, particularly among lizards and birds (e.g. Brattstrom, 1974; Watson and Moss, 1970).

Territorial social organization is shaped by aggressive behavior. Individual aggressiveness may be causally important in the ability to procure superior territories. There is scant knowledge, though, of the role of aggression during the procurement of a territory. Do the more aggressive individuals secure better territories, or do they become more aggressive after gaining their territories? A need thus

exists for a study of individual aggressiveness, as it might influence the procurement of superior territories.

Objective

The main objective of this study was to establish the role of aggression in the acquisition of superior home ranges among juvenile Desert Side-blotched Lizards Uta stansburiana stejnegeri, through the use of exogenous testosterone subdermally implanted. This species was used because these animals are small, sedentary, aggressive toward conspecifics from birth, diurnal, and are easy to observe, mark, and capture. Because of its natural abundance at the study site, a fairly large sample size was also possible. The form of territoriality in Uta is also common to many other vertebrates, so the relationships between aggression and territoriality in this species could generalize to other vertebrate groups. This species is easy to manipulate experimentally; it can tolerate perturbances and behave normally during field studies. Finally, Uta stansburiana has been intensively studied by others, and many aspects of its behavior and general ecology are well known. Its territorial behavior also has been well studied and documented (Tinkle, 1967; Fox, 1973, 1978; Fox, Rose, and Myers, 1981).

Another objective of this study was to examine the effects of exogenous testosterone on the reproductive structures of the gonads and kidneys and on blood levels of testosterone in both juvenile male and female Uta. Effects of testosterone

implantations on the reproductive cycle of adult Uta have been noted (Ferguson, 1966), but no studies have been attempted using juveniles. Testosterone implant studies have also been conducted on other adult iguanids (Forbes, 1941; Evans, 1957; Mason and Adkins, 1976; Crews, 1974), as well as on skinks (Reynolds, 1943; Done and Heatwole, 1977), juvenile turtles (Evans, 1940), and alligators (Forbes, 1938).

Adult Uta in the area studied are territorial: they defend their exclusive areas of familiarity against other conspecifics (Brown and Orians, 1970). Juvenile Uta occupy home ranges, which, as the lizards mature, they begin to aggressively defend. Some portions of the home range are more vigorously defended than others (Tinkle, 1967). We can thus refer to a juvenile's area of familiarity in two ways: as home ranges with some defense of certain areas, or as territories with a considerable amount of overlap between individuals. To avoid confusion in this paper, juveniles will be considered to possess home ranges; hence, the main concern was with home ranges during the study. Home range is methodologically a more accurate term, since no attempt was made to plot points of defense between juveniles.

Major Hypothesis

Dominance in juvenile Uta has been correlated to possession of a superior home range (Fox, Rose, and Myers, 1981). Similarly, in a study involving adult scincid lizards, subordinate lizards receiving testosterone proprionate im-

plants became increasingly aggressive and eventually obtained a higher position in a social dominance hierarchy (Done and Heatwole, 1977). The major hypothesis of this study, then, was that aggression influences the acquisition of superior home ranges in juvenile Uta. Initially aggressive juveniles should obtain a superior home range. After implants of testosterone, lizards should become increasingly aggressive and increase the quality of their home ranges. The implanted lizards should show a significant increase in the size of gonads and in secondary sexual structures of the kidneys over unimplanted individuals. Testosterone levels in the bloodstream of implanted lizards should be significantly higher.

Value of Study

Although the nature and subject of aggression has undergone extensive research and discussion in the past, this study helped to broaden the base on which future research can be conducted. This might include further enquiry into the cause and effect between aggression and home range quality by altering home range quality, using electrophoresis to examine the inheritability of aggression, and comparing the home range quality among relatives.

Another potential experiment is the converse of the present study. By tranquilizing or castrating individuals with known home range quality, the effect of a decrease in aggressive levels upon ability to keep a superior home range or territory may be seen. Such an experiment has been attempted

using male Red-winged Blackbirds (Peck, 1972), but none have been conducted using lizards, which would appear to be better subjects since they are sedentary and much easier to observe and study.

A more complex and subtle experiment would be to examine the relationship between an individual's level of aggression and the size and degree of development of its gonads and reproductive structures of its kidneys. Apparently, only one study of this type has been conducted using lizards as subjects (Brackin, 1978).

Finally, this study adds to the knowledge concerning aggression and territoriality by viewing behavior on three biological levels: behavioral, physiological, and anatomical.

Summary of Research Problem

Territoriality is common to many vertebrate groups. Possession of a territory enhances individual fitness. There is a correlation between level of aggression and acquisition of a superior territory, but little is known of the role played by aggression during the development of territoriality. This study further defined this role in juvenile Desert Side-blotched Lizards. The major hypothesis tested was that aggression plays a major role in the acquisition of a superior home range. Juvenile Uta occupy home ranges which develop into territories as the animals mature. Another objective was to examine the effects of testosterone implantations on the gonads and kidneys in both sexes and on hormone level present in the cir-

culatory system. This study viewed aggression on three levels:
behavioral, physiological and anatomical.

CHAPTER II

LITERATURE REVIEW

Introduction

Territoriality plays a major role in determining the reproductive success of individuals of certain animal populations, including many avian and reptilian. Usually, a superior territory helps to assure reproductive success and survival for the individual. As the concept of territoriality has grown, so also has discussion concerning its major functions. Wynne-Edwards (1962) and Kluijver and Tinbergen (1953) claimed that territoriality functioned chiefly in regulating population size. Territoriality, they felt, prevented overpopulation and thus guarded the population from an excessive fluctuation of numbers. In contrast, many studies have shown an inverse relationship between density and territorial size or home range size in many species (Philibosian, 1975; Morse, 1976; Stenger, 1958; Holmes, 1967; Milstead, 1970), including Uta stansburiana (Worthington and Arviso, 1973). Population regulation is now thought to be a by-product of territorial behavior (Wilson, 1975), since most territories change inversely to resource abundance. The fitness of a territory holder is enhanced for a variety of reasons; the function of territories is probably multiple.

Territorial Size, Environmental Resources,
and Individual Fitness

Territorial size has been shown to fluctuate inversely with abundance of resources (loc. cit.). Simon (1975), working with the lizard Sceloporus jarrovi, experimentally demonstrated that territory size was inversely correlated with the abundance of food. Other studies have shown that individuals with more optimal territories, and thus greater resource abundance, grow larger (Boag, 1973), survive longer (Fox, 1973), and produce more offspring (Tinkle, 1969) than those on sub-optimal territories. Adult male S. jarrovi increased home range sizes and decreased the amount of overlap between home ranges as the fall breeding season approached (Ruby, 1978). An optimal territory seems often to increase the chances of an individual securing an adequate share of environmental resources. Possession of a superior territory enhances individual fitness often by increased survival (Watson and Moss, 1970; Krebs, 1971). Territories, then, can be defined as being selectively maintained on the basis of advantages to individuals within a population (Brown and Orians, 1970; Krebs, 1971; Wilson, 1975).

Aggression and Territorial Quality

The degree of aggression an individual shows may be important in determining its territorial quality. The most dominant Red Grouse cocks in a population were the most aggressive and hence secured the best territories (Watson and

Miller, 1971). These cocks also had the best chance of surviving until the next breeding season. Adelie Penguins which displayed optimum nesting success in a population had high aggressiveness scores and secured the best territories in the center of a nesting colony (Spurr, 1974). Coulson (1968) found a similar situation in kittiwake colonies. Usually, the more dominant and aggressive individual secures the territory, often excluding subordinates to habitats of lesser quality (Krebs, 1971; King, 1973). Conversely, tranquilized male Red-winged Blackbirds were unable to defend their territories against more aggressive newcomers, and subsequently lost them (Peck, 1972).

The same relation between aggression and territorial quality appears to hold true with lizards. In iguanid lizards, aggression functions in establishing the social structure of a population (Carpenter, 1967). Dominance may determine if a male lizard will court and breed. A dominant male on his own territory is more likely to breed than are subordinates (Carpenter, 1980). Blair (1960) found that male Rusty Lizards (Sceloporus olivaceus) who had survived more than two breeding seasons aggressively excluded yearling males from breeding territories. In a study of territoriality of the fence lizard, Sceloporus occidentalis, aggression of stronger lizards toward weaker individuals was one of the major factors influencing territorial shifting (Fitch, 1940). Others also have reported a correlation between levels of aggression and territorial size as well as with position in a dominance

hierarchy (Brattstrom, 1974; Boag, 1973; Ferner, 1974; Brackin, 1978; Stamps, 1978). The intensity of aggressive behavior between two individuals is often a function of the territorial status of the participants (Ruibal and Philibosian, 1974). Dominance in juvenile Uta was associated with home ranges which increased an individual's chance of survival (Fox et al., 1981). Sub-adult Anolis lineatopus were socially excluded from optimal habitat due to the territorial behavior of adults (Rand, 1967a). Dominant chuckwallas (Sauromalus obesus) were the most aggressive individuals and also tended to form stable territories which they retained for several seasons (Berry, 1974). Aggressiveness therefore is linked intimately with territoriality in many lizard and bird species.

Hormonal Control of Aggressiveness

It can be speculated from studies correlating aggression with reproductive behavior that sexual hormones play an important role in determining individual aggression (Barfield, 1967). The injection or implantation of androgens should alter an animal's agonistic behavior.

Injections of testosterone propionate induced adult male behavior and increased aggression in female and immature Black-crowned Night Herons (Noble, Wurm, and Schmidt, 1938). It appears that sex hormones lower the threshold for the expression of agonistic behavior (King, 1973). Testosterone propionate implants in the brains of Ring Doves produced an increase in both copulatory and aggressive behavior (Barfield,

1971). No behavioral changes were noted when cholesterol implants were used as a control. In some birds, luteinizing hormone influences agonistic behavior (Crooks and Butterfield, 1968).

Implantations of testosterone propionate into reptiles have been shown to stimulate masculine morphological development (Forbes, 1938, 1939, 1941; Noble and Greenburg, 1941; Reynolds, 1943; Prasad and Sanyal, 1969), to increase courtship and aggression in both male and female individuals (Evans, 1940, 1952, 1957; Crews, 1974, 1975) and juveniles (Evans, 1957), as well as adult Uta stansburiana (Ferguson, 1966). Testosterone treatment of subordinate male scincid lizards (Sphenomorphus koscinski) increased their aggressiveness and caused them to exhibit increased sexual activity (Done and Heatwole, 1977). Temperature has been shown to affect the uptake of androgens in Anolis carolinensis, and consequently plays an important part in social behavior (Pearson, Tsui, and Licht, 1976). In the six-lined racerunner (Cnemidophorus sexlineatus), most subordinate males exhibited atrophy of reproductive organs and were less active sexually (Brackin, 1978).

Sex hormones also appear to be important in maintaining individual aggressiveness. Daily injections of testosterone to the least aggressive Ring Doves in a social situation elicited an obvious change in the dominance hierarchy (Bennett, 1940). The injected birds formed a dominant, despotic relationship with the other birds which lasted until the injections were stopped. The same results were found with

domestic hens (Allee, Collias, and Lutherman, 1939). In skinks, as the effect of administered testosterone diminished, treated male lizards returned to their former subordinate status (Done and Heatwole, 1977).

Inducement of Territorial Aggression

Until the present, no field studies on the inducement of territorial aggression through androgen implantations had been attempted with lizards. However, several studies have been conducted using birds as subjects. Red Grouse cocks dramatically increased their aggressive levels when they were implanted with testosterone, which in turn had a profound influence on their social status (Watson and Moss, 1972). Two territorial cocks receiving implants greatly increased their aggressive levels and their territory size. Two non-territorial cocks receiving testosterone aggressively took territories from other cocks. They retained these territories for several years. One cock, implanted with estrogen, eventually lost both its mate and its territory. Trobes and Oring (1972) were unsuccessful in their attempt to alter lek behavior in Sharp-tailed Grouse through testosterone implants because of the lateness in the breeding season. Implanted males, though, did increase their aggression, as well as extend their activity on the lek grounds well past the breeding season. Hormone implants did not increase aggression in the Great Tit (Krebs, 1971).

CHAPTER III

MATERIALS, METHODS, AND PROCEDURE

Field Procedure

A population was studied in its natural habitat in west Texas. The data were collected on an area of approximately 0.5 hectares, eight kilometers south of Kermit, Winkler County, Texas. The site is at an elevation of 885 meters and is located along the ecotone of short-grass prairie and Chihuahan Desert. The dominant vegetation is mesquite (Prosopis juliflora), yucca (Yucca glauca), broomweed (Xanthocephalum microcephalum), croton (Croton dioicus), and dropseed grass (Sporobolus flexuosus). The plant cover is only 20% of the total area (Tinkle, McGregor, and Dana, 1962). The remainder is bare aeolian sand, although short-term weather conditions can affect the amount of ground cover. The region is characterized by hot, dry summers where daily temperatures often exceed 38°C., and by mild winters. The average rainfall varies annually from 25 to 40 cm (Fox, 1973).

Two enclosed experimental plots of 0.2 hectares each were used on the study site. On each was a population of juvenile Uta at densities within ranges reported by Tinkle (1967) at this site. A grid of numbered stakes at intervals of 7.5 meters was set on each plot. The plots were enclosed by

galvanized sheet metal extending about 15 cm below the ground surface and about 85 cm above the ground. Supporting stakes were located outside the fence and capped with sheet metal, minimizing loss of subjects through escape.

When first captured, each lizard was marked both by clipping toes and by application of four acrylic paint spots to the dorsum. Three toes were removed from each lizard: no more than one toe per foot, and only the extreme tip of the toe basal to the nail was clipped. The paint was applied by syringe: six colors were used but not more than two were used on any individual. The paint was re-applied after each molt.

The grids were walked six days a week, each morning and evening. These are the times Uta is most active during the summer (Irwin, 1965; Tinkle, 1967; Fox, 1973, 1978). All vegetation was shaken and all boards and other debris were lifted to census as many lizards as possible. A portable trap designed by Fox (1973) was used to capture any unmarked individuals. When a color-marked lizard was found, the following data were recorded without capture: grid position, time, date, temperature, and the type of vegetation or debris the animal was seen under or adjacent to. When a lizard was captured its snout-vent length, total length, and any evidence of tail loss was noted. All snakes and other reptilian predators were removed from the enclosures. The enclosures were routinely walked at night to remove any snakes which might have entered.

A total of 67 juveniles were seen 4 or more times (mean=9.96 sightings/lizard) in the first stage of the experiment.

After implantation, only 41 lizards were seen 4 times or more (mean=9.15 sightings/lizard) due to natural deaths.

Home ranges, using the convex polygon technique, were constructed both before and after implantation using only those animals which had been seen at least four times. This is the minimum number of observations needed to adequately determine a juvenile Uta's home range (Tinkle, 1967; Fox, 1973, 1978), although most lizards exceeded 9 sightings; more sightings appear to add little additional area. Waldschmidt (1979) found no significant relationship between home range size and number of sightings in adult Uta using this method.

Once the home ranges of all juveniles had been constructed, their area and home range quality was calculated. Counts of all plant species, boards, mammal burrows, insect holes, and ant nests of large and small species were made within a two or three day interval of no rain, so insect holes and ant nests were comparable among different home ranges. The cover area of mesquite and yucca was measured for each home range. A multivariate linear discriminant function index used by Fox et al. (1981) was employed to combine the elements of each home range into a composite measure of home range quality based on survivorship potential. Fox's method appropriately weighted each variable so as to maximally separate survivors from nonsurvivors along a composite axis. The coefficients from Fox's discriminant function were then applied to the data of this study. This process created multivariate indices of home range quality for the present study using features that

had been previously associated with survival (Fox et al., 1981).

Over the same period the implant experiment was conducted, home range quality measurements of an enclosed, unmanipulated, control population of juvenile Uta were determined in another study by Fox (pers. comm.). Unfortunately, the discriminant function generated by Fox et al. (1981) was not suitable for distinguishing the home ranges of survivors from nonsurvivors in the control plot in 1979. A new function was generated from the home range measurements and survival of the control population and was retroactively applied to the home range data of the experimental lizards. Since survivorship could not be determined until the end of the study season, the new function could not be used in the original design of the implant experiment. Using this function, most testosterone implants, by chance, came from home ranges of high overall quality rather than low (7/9 implant pairs) as originally planned. Nevertheless, the experiment can still test the hypothesis that testosterone will increase aggression and result in increased success at securing superior home ranges compared to controls.

Once the home range quality for each lizard was measured, the animals were removed from the enclosures and pair-matched according to snout-vent length and sex. The pairs were allowed to interact in a neutral arena until their relative aggression was determined. The arena (1.5 m. diameter) consisted of sand substrate with a yucca located in the center under a heat lamp, thus giving the arena some desirable features of natural habitat. The paired lizards were interacted with each other

for at least one hour or until relative aggression of the two lizards became distinct. Relative aggression was defined by the tabulation of frequency of aggressive patterns (pushups, lateral displays, circling, attacks or bites, supplants, and superimpositions) minus the sum of submissive postures (flattening) of one lizard directed against the other. An unweighted sum was computed and assumed to directly reflect level of aggression against the pairmate. This method has been shown to be successful in quantifying aggression in displaying lizards (Evans, 1936a, 1936b; Carpenter and Grubitz, 1960; Brattstrom, 1974; Fox et al., 1981).

From one enclosure one lizard from each pair was implanted subdermally with a pellet of testosterone (1.14 to 2.17mg/gram lizard weight). Their pair-mates received only silk suture thread (sham). All the lizards from the other enclosure were implanted with silk suture thread as a sham control. Cholesterol was not used as a control due to indications that it might have an inhibitory effect on androgen target sites (Mays, Boydston, and Fox, in prep.). After 48 hours spent in post-operative recovery, the lizards from one enclosure were transferred to the other and vice-versa, thus exposing all lizards to novel habitat. The lizards were again censused for one month. Some new lizards were introduced into the enclosures to bring lizard densities up to the pre-implant stage but were not utilized as subjects in the experiment.

Home range sizes and qualities were measured for all surviving experimental subjects as before. The lizards again

were interacted by pairs in a neutral arena. They then were sacrificed and prepared for endocrinological and histological assay.

Radioimmunoassay Procedure

The amount of plasma testosterone (and dihydrotestosterone) was measured in the subjects via radioimmunoassay using a highly specific antiserum prepared from rabbits against testosterone-3-oxime-bovine serum albumin. The New England Nuclear Testosterone ^3H Radioimmunoassay Pak was used for the assay.

Blood from individuals was pooled according to sex and treatment, centrifuged, and the plasma separated from other blood components. To an aliquot (.075--.250ml) of plasma was added enough distilled water to bring the volume to 1.00ml. Recovery tracer (0.1ml) was added to each sample, as was 10ml of methylene chloride. After agitation, the aqueous phase was carefully aspirated and the extract serially washed with 1.0ml of 0.1N NaOH, 0.1N acetic acid, and water to remove potentially interfering substances. The final methylene chloride extract was dried under a gentle stream of air. Testosterone was concentrated in the tip of the test tube through multiple washings with ethanol and redrying.

The dried fractions were redissolved in 2.0ml of ethanol. For the assay, 0.1, 0.2, and 0.4ml aliquots, in duplicate, were transferred to assay tubes and dried down. The remaining solution was used in recovery calculations. To the dried ali-

quots, 0.1ml of assay buffer was added. Then 0.1ml of assay tracer was added followed by 0.1ml of antiserum. Standard testosterone solutions ranging from .005--4.0ng/0.1ml buffer also were mixed in duplicate along with the unknown samples. After incubating for 12 hours at 4°C., separation of free from bound testosterone was accomplished by adding dextran coated charcoal. The samples were centrifuged and the supernatant transferred to scintillation vials. Ten ml of scintillation solution was added to each vial and shaken. The vials were counted in a Beckman Liquid Scintillation Counter for 50 minutes. A "blank" and a 0 standard vial provided a check on the system.

Anatomical Procedure

The experimental subjects were captured and weighed after completion of the field study. The animals were sacrificed and their blood removed for use in the radioimmunoassay. The reproductive organs and kidneys were immediately dissected out and the reproductive organs weighed on a precision Mettler Balance accurate to 0.01mg. A gonadosomatic index (GSI) was calculated for each lizard. The remainder of the testosterone pellet in some lizards also was weighed. The tissues were fixed in Bouin's solution, cleared and dehydrated in isopropyl alcohol and xylene, embedded in paraffin, and sectioned in 7-9 micron thicknesses. They were stained using Harris' haemotoxylin and eosin. Measurements of the tubule diameter, lumen diameter, epithelial cell height, and the degree of granulation

were made of the sexual segment of the kidney using a micrometer eyepiece. In the males, the lumen diameter, tubule diameter, and epithelial height of the epididymis also were measured. The seminiferous tubule diameter was measured and the presence of sperm in the testes noted. In females, the diameter of the largest follicle was measured and the oviduct examined for development.

CHAPTER IV

RESULTS

The field experiment can be divided into two separate phases: a pre-implant and a post-implant phase. No significant differences in snout-vent length existed between testosterone implants and shams (t-test, $p > .05$). The treatment and control groups, then, can be considered to be of equivalent ages and any differences noted to be independent of age or size.

Endocrinology

Testosterone Radioimmunoassay (RIA)

The amount of testosterone and dihydrotestosterone (pooled) present in the blood plasma of the subjects varied according to sex and type of implant. Testosterone implants for both sexes showed elevated levels of plasma testosterone compared to similar aged shams (Table I).

Histology

The sexual segment (the hypertrophied tertiary collecting ducts) of the kidney normally is developed only in adult males with spermatogenically active testes. In Uta, it is regressed during sexual quiescence (Asplund and Lowe, 1964). Testosterone

TABLE I
 RADIOIMMUNOASSAY OF TESTOSTERONE PLUS
 DIHYDROTESTOSTERONE IN BLOOD
 PLASMA OF SUBJECTS POOLED
 ACCORDING TO SEX AND
 IMPLANT*

	Male (ng/ml)	Female (ng/ml)
Testosterone Implant	119.4	58.5
Sham Implant	14.1	15.6
Hatchlings	7.2	4.7

*Average Deviation = \pm .042 ng/ml

Average deviation was calculated by finding the difference of each standard solution sample (N=26) with known testosterone titers from the standard curve. Differences (in ng/ml) were read directly off the curve, added together, and the sum averaged. The average was halved to show deviation both above and below curve.

treatment stimulated development of the sexual segments in both males and females to a state similar to that of a sexually active adult male (Figure 1). Shams displayed no such development. The hypertrophied collecting ducts in the testosterone females (the newly formed sexual segment) histologically were identical to those in the males (Figure 2). Testosterone-implanted males and females both displayed significantly larger tubule and lumen diameters than shams (Table II). The sexual segment tubules of the testosterone implants were lined with columnar epithelial cells with secretory granules located primarily in the apical portion. The columnar epithelial cell height differed significantly according to the implant received in males and very nearly so in females. The granules were much more numerous in the treated males than in the treated females. The degree of granulation was different between testosterone males and shams, but was not significantly different in females. The epithelium of the testosterone males was comparable to that shown by normal adult males displaying secretory activity during the breeding season. Testosterone females tended to show slightly less hypertrophy of the sexual segment than did testosterone males.

The testosterone-implanted lizards had significantly larger gonadosomatic indices (GSI) than the shams, both for sexes separate and for sexes pooled (Table III).

The testes and epididymis of the testosterone males differed from the sham males in several of the variables measured (Table IV). The epididymis of the implants was



A

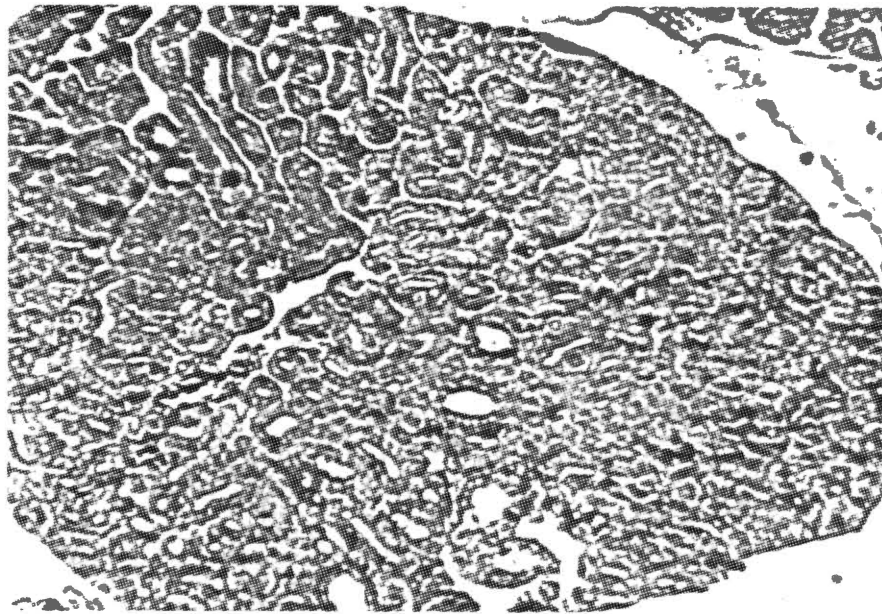


B

Figure 1. Differences in Male Kidney Structures Between A) Testosterone Implant and B) Sham Implant (x40)



A



B

Figure 2. Differences in Female Kidney Structures Between A) Testosterone Implant and B) Sham Implant (x40)

TABLE II
DIFFERENCES IN "SEXUAL SEGMENT" STRUCTURES OF THE KIDNEY BETWEEN TESTOSTERONE IMPLANTS AND SHAMS BY SEX

	Testosterone			Sham			p ^a
	N	x	SD	N	x	SD	
Tubule Diameter (μ)							
Males	5	20.84	4.56	9	8.91	1.36	< .01
Females	4	17.04	3.56	19	8.48	0.86	< .05
Lumen Diameter (μ)							
Males	5	10.67	2.70	9	5.39	1.19	< .05
Females	4	9.92	0.97	19	5.17	0.18	< .001
Epithelial Cell Height (μ)							
Males	5	5.32	1.62	9	1.72	0.27	< .01
Females	4	3.68	1.57	19	1.47	0.19	< .10
Epithelial Cell Granulation (1-5)							
Males	5	1.00	0.00	9	4.76	0.32	< .001
Females	4	3.75	1.35	19	5.00	0.00	NS

^a Student's t-test, corrected for unequal variances where appropriate

TABLE III
 COMPARISONS OF GONADOSOMATIC INDEX (GSI)
 BETWEEN TESTOSTERONE IMPLANTS AND
 SHAMS FOR EACH SEX SEPARATE
 AND SEXES POOLED

	N	Median	U ¹	p
♂♂-Testo	5	1.59	42	< .01
♂♂-Shams	9	1.14	3	
♀♀-Testo	4	2.64	159.5	< .001
♀♀-Shams	19	0.97	2	
♂♀-Testo	9	2.17	238	< .001
♂♀-Shams	28	1.04	14	

¹ Mann-Whitney U statistic: larger U means most values are larger for that group.

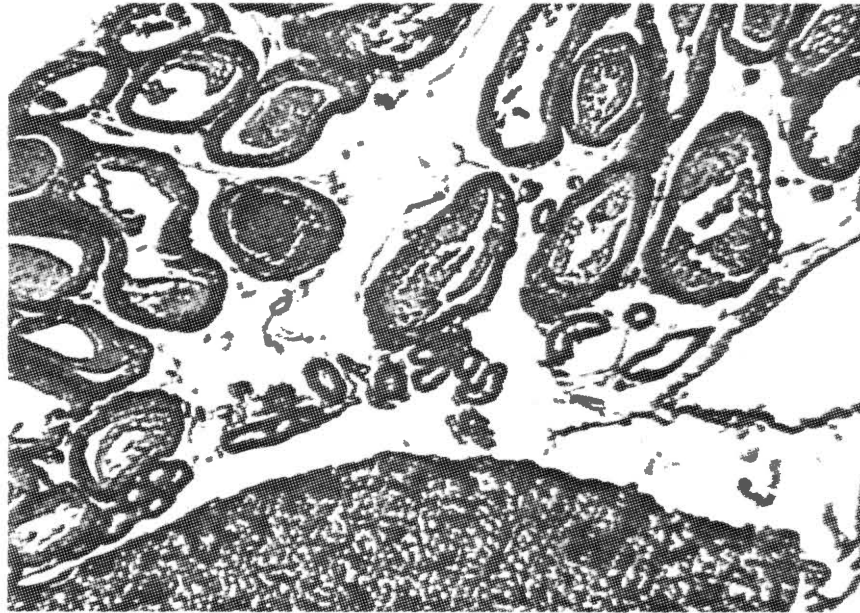
TABLE IV
DIFFERENCE IN MALE GONADAL STRUCTURES BETWEEN
TESTOSTERONE IMPLANTS AND SHAMS

	Testosterone			Sham			p ^a
	N	x	SD	N	x	SD	
Epidydymis: Epithelial							
Cell Height (μ)	4	2.06	0.32	8	1.11	0.22	< .001
Epidydymis: Lumen							
Diameter (μ)	4	11.22	2.91	8	4.31	1.44	< .001
Epidydymis: Tubule							
Diameter (μ)	4	12.97	2.07	8	6.65	1.85	< .001
Testis: Seminiferous							
Tubule Diameter (μ)	4	7.00	0.48	8	7.77	2.06	NS

^a Student's t-test, corrected for unequal variances where appropriate

significantly enlarged in terms of tubule and lumen diameters as well as epithelial cell height. The epididymal appearance of the testosterone males was quite similar to a sexually active adult male. Increased cytoplasmic granulation, columnar epithelial cells with round, basally located nuclei, and thin connective tissue capsules all served to distinguish the epididymal tubules of the implants. Evidences of secretory activity could occasionally be noticed. Shams had proportionately thicker capsules, cuboidal epithelium with centrally located nuclei, and non-granulated cytoplasm. No differences in seminiferous tubule diameter of the testis of testosterone versus sham males were seen. Although not quantified, the number of seminiferous tubules was markedly greater in the implants. The testosterone implants also showed more extensive spermatogenesis. There were many more primary and secondary spermatogonia in the testosterone implants (Figure 3), although the number and degree of development were considerably less than in an adult male. Shams tended to have more interstitial connective tissue present in the testes. No mature sperm could be found in either implant group.

There were several differences in female gonadal structures between testosterone implants and shams (Table V). In testosterone females the diameter of the largest follicle was increased significantly over the largest sized follicles in the sham individuals. No apparent differences in the histology of the follicle between the implant groups was noticed. Testosterone females had fairly well developed oviducts, while



A



B

Figure 3. Differences in Male Gonadal Structures Between A) Testosterone Implant and B) Sham Implant (x40)

TABLE V
DIFFERENCES IN FEMALE GONADAL STRUCTURES BETWEEN
TESTOSTERONE IMPLANTS AND SHAMS

	Testosterone			Sham			p
	N	x	SD	N	x	SD	
Diameter of Largest Follicle (μ)	4	130.25	20.03	14	83.28	21.16	<.01 ^a
Ability to Distinguish Oviduct from Surrounding Mesotubarium	4	$\frac{\text{yes}}{3}$	$\frac{\text{no}}{1}$	14	$\frac{\text{yes}}{1}$	$\frac{\text{no}}{13}$	<.05 ^b

^a Student's t-test

^b Sign test

shams had small oviducts which usually could not be distinguished from the surrounding mesotubarium. No oviduct observed was similar to an adult female.

Behavior and Home Range Ecology

Aggression

Before implantation, differences in individual aggression of testosterone lizards and shams were insignificant (Table VI). At the end of the post-implant stage, those lizards receiving testosterone showed significantly increased aggressive levels. Shams displayed no change in aggressive levels.

Home Range Ecology

Although most of the testosterone implants originated from superior, rather than inferior home ranges as planned (due to reasons explained previously), the experiment can still determine whether acquisition of a superior home range in a novel habitat is related to hormonal treatment. Testosterone implants displayed a marked increase in the size of their home ranges from the pre-implant through the post-implant stage (Table VII). Home range quality (HRQ) changes induced by the treatment of exogenous testosterone were analyzed by a non-parametric, paired design. For each plot, differences in final home range discriminant scores of the sex and size matched pairs were computed. For the treatment plot, these

TABLE VI
 ARENA DETERMINED AGGRESSIVE SCORES BEFORE
 AND AFTER IMPLANTATION

Treatment	Before			After			p ^a
	N	U	(Median)	N	U	(Median)	
Testosterone	8	12.5	(9.5)	7	43.5	(17.0)	<.05
Sham	12	84.0	(5.0)	11	48.0	(5.0)	NS

^a One-tailed Mann-Whitney U-test.

TABLE VII
 CHANGE IN HOME RANGE AREA OVER THE
 EXPERIMENT (SQUARE METERS)¹

Testosterone Implants (N=9)	All Shams (N=21)	
-31.77	-66.24	+9.96
+5.62	-26.92	+11.57
+7.95	-15.81	+14.95
+18.20	-4.90	+16.74
+48.21*	-3.69	+19.11
+58.63	-2.35	+21.02
+79.68	-0.84	+22.35
+83.90	-0.79	+32.50
+126.82	+1.62	+43.72
	+5.61	+71.50
	+7.86*	

¹ Mann-Whitney U test: $U=140$; $t_s=2.06$; $p<.05$, two-tailed.

* Median

differences were computed as testosterone implants (initially high HRQ) minus shams (initially low HRQ). For the control plot, the differences were computed as shams that originally inhabited high quality home ranges, minus shams that originated from low quality home ranges. The treatment paired differences were then compared to the control paired differences by a Mann-Whitney U-test. Individuals with testosterone treatment were able to reacquire higher quality home ranges in novel habitat than shams with originally similar home range experience (Figure 4). In the treatment plot, both the testosterone implants with initially high HRQ scores and their pair-mates with originally low scores improved the quality of their subsequent home ranges. In the control plot, however, lizards with originally low HRQ subsequently gained high quality home ranges, whereas those with initially high HRQ subsequently fell to low quality home ranges (Table VIII).

Summary of Results

The testosterone-implanted individuals displayed considerably higher testosterone levels in their blood plasma than others. Sham implants were next highest, followed by hatching controls. Testosterone implants showed hypertrophy of the sexual segment of the kidney, significantly larger tubule and lumen diameters, more well developed epithelial cell linings and, in males, a higher degree of cellular granulation. Testosterone males also had significantly more developed epididymal structures than did the sham males. No significant difference

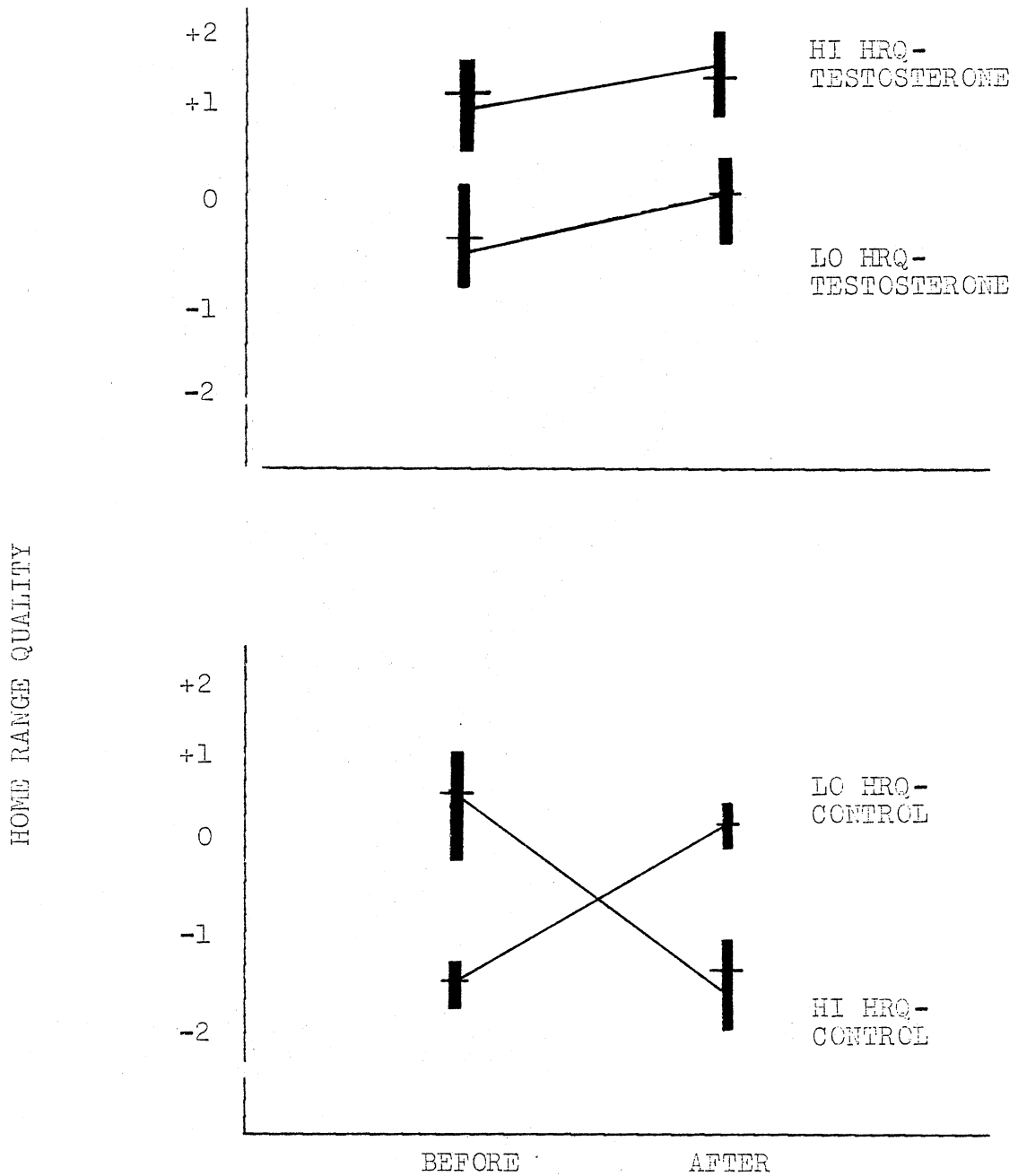


Figure 4. Mean Home Range Quality (HRQ) of Treatment Groups Before and After Hormone or Sham Implantation. Horizontal Bars are Means; Wide Vertical Bars are Standard Errors of Means

TABLE VIII

CHANGE IN HOME RANGE QUALITY (HRQ) OVER
THE EXPERIMENT, COMPARING INITIALLY
HIGH HRQ LIZARDS SUBSEQUENTLY IM-
PLANTED WITH TESTOSTERONE WITH
INITIALLY HIGH HRQ LIZARDS
SUBSEQUENTLY SHAM-IMPLANTED

Testosterone ¹		Sham ²	
Initially High HRQ	Initially Low HRQ	Initially High HRQ	Initially Low HRQ
+2.78	+2.09	+0.88	+2.84
+2.07	+1.94	-1.04	+1.92
+0.54	+1.88	-1.48	+1.36
+0.17*	+1.60	-2.78	+1.17
-0.89	-1.15	-2.95	-0.62
-2.74	-2.21	-3.41	-0.83
-3.11			

¹ Mann-Whitney U test: $U=27$; $p>.05$, two-tailed.

² Mann-Whitney U test: $U=34$; $p<.05$, two-tailed.

* Median

was found in seminiferous tubule diameters. Testosterone females had larger follicles than shams as well as a higher degree of development of the oviducts.

The lizards selected for testosterone implants initially displayed no significant difference in aggressive levels with their sham pair-mates. At the end of the experiment, all those receiving testosterone displayed significantly higher aggressive levels while the sham implants did not.

Testosterone-implanted individuals, when placed in a novel habitat, showed a larger increase in home range area than shams. The testosterone implants acquired significantly better quality home ranges than their sham pair-mates when compared to the sham pairs of the control plot. In the control plot, those with originally high quality home ranges obtained lower quality home ranges in the novel habitat. Such an effect did not occur among those lizards in the treatment plot with initially high quality home ranges that were implanted with testosterone.

CHAPTER V

DISCUSSION

Endocrinology

Testosterone Radioimmunoassay

Exogenous testosterone implantation had a dramatic effect upon plasma hormonal levels. The testosterone lizards had considerably higher hormone levels than the shams; unquestionably, the implant technique succeeded.

However, despite the fact that males and females received approximately equal doses of testosterone, the male implants displayed hormone titers over twice that of the females. One explanation may be the exogenous testosterone stimulated further production of testosterone in male implants. In vivo hormone production in males, though, would have to be very high to account for the difference in titer levels between the sexes. Perhaps the production of testosterone is maintained (but not initiated) by the presence of a minimal testosterone level in the bloodstream. However, negative feedback of testosterone on LH (Luteinizing Hormone) release should result in a decrease of further testosterone production.

Another more logical possibility is the female implants may have synthesized some of the exogenous testosterone into

estrogen, since testosterone is one of the precursors of this hormone. The estrogen may have been at least partially responsible for the hypertrophy of the oviduct, since both these hormones can stimulate this structure (Prasad and Sanyal, 1969; Noble and Greenburg, 1940). An estrogen radioimmunoassay would be sufficient to test this hypothesis.

Histology

Exogenous testosterone applied to juveniles significantly increased the gonadosomatic indices of both sexes. Likewise, Noble and Greenburg (1940) found an increase in gonad weight after administering testosterone propionate to immature and adult Anolis. No such effect was seen in Hemidactylus (Prasad and Sanyal, 1969). Both sexes also developed hypertrophied sexual segments of the kidney. The development of the sexual segment is initiated, if not maintained, by testosterone. Other studies also indicate the sexual segment is hypertrophied by androgen treatment (Noble and Greenburg, 1940, 1941; Reynolds, 1943; Prasad and Sanyal, 1969).

Development of the sexual segment was more pronounced in the males than in the females. Secretory granules could be found in the cytoplasm of the tubule epithelium more often and in greater quantity in the males. Few secretory granules were noticed in the epithelial lining of females. Epithelial and glandular activity also were stimulated in this study. A similar phenomenon has been observed in Hemidactylus (Prasad and Sanyal, 1969). Results indicate a differential sensitivity

of the homologous target sites of the sexes to androgens. Males are apparently much more sensitive to testosterone than females; whether this is true of other steroids is not yet fully understood. Some studies indicate the sexual segment in males is sensitive to estrogen injections, but not to as great a degree as that produced by testosterone (Reynolds, 1943). Other studies report that estrogen does not stimulate the sexual segment (Forbes, 1941).

The androgen treatment stimulated development of various male reproductive organs. It seems as though testosterone plays a role in the development of the testis, but the role is not a major one; other hormones may play a part in testis development. The development, if not maintenance, of epididymal structures also appears at least partly dependent on testosterone. The major changes resulting from implantation of testosterone are the initiation of secretory activity and an increase in the size of the various tubular components of the reproductive structures. The initiation of spermatogenesis is not under the control of testosterone.

Reproductive accessory structures of female testosterone implants also varied considerably from their sham controls. Follicle and oviduct development were significantly increased in the testosterone implants. Testosterone implants, had, in general, a greater degree of development of the oviduct, although not as great as in a normal adult female. Oviduct development could also be due to the influence of estrogen (explained above). The stimulation of the oviduct by testo-

sterone and estrogen have led some to consider the possibility that the oviduct of reptiles could be regarded as an "ambisexual substrate," whose development depends on either hormone (Prasad and Sanyal, 1969). Because of the small size of the sham implants' oviducts, no attempt was made to compare oviduct weight. It seems reasonable, though, that the oviducts from the testosterone implants weighed more because of the increased development. Oviducts of adult female Anolis implanted with testosterone displayed an increase in weight over controls (Noble and Greenburg, 1940).

Ovarian weight and size of the largest follicles were significantly increased compared to the shams. Such an increase in ovarian weight was observed by Noble and Greenburg (1940) after testosterone administration in Anolis, but not in Hemidactylus (Prasad and Sanyal, 1969). No follicle seen in the testosterone implants approached the size of the follicles in a mature female.

Behavior and Home Range Ecology

Aggression

Juvenile Uta live in a very competitive environment (Tinkle, Wilbur, and Tilley, 1970). Survival may depend on a number of factors, including home range features and aggression (Fox, 1978; Ferguson and Bohlen, 1978; Tinkle, 1965, 1969). More aggressive juvenile Uta occupy better quality home ranges than less aggressive individuals (Fox et al., 1981). The

testosterone implant field experiment suggests that increased levels of aggression aid in acquisition of superior home ranges which, in turn, enhance survival.

A previous study corroborates this interpretation (Fox et al., 1981). When dominant-subordinate juvenile Uta were introduced pair-wise into small outdoor pens with halves of different habitat quality, the more aggressive lizards spent significantly more time in the superior habitat than did the less aggressive. In this study, testosterone implants increased their aggressive levels. When those lizards were exposed to new habitat in competition with shams, they more successfully acquired superior home ranges compared with the sham pairs of the control plot.

Other studies have shown that aggression appears to be an essential element in lizard social systems (Brattstrom, 1974; Stamps, 1978; Simon and Middendorf, 1980). Size of territories in Lacerta muralis varied directly with the aggressive level of the individual (Boag, 1973). The more aggressive the lizard, the larger territory it possessed. Adult Uta aggressively partition available habitat into discrete territories (Tinkle, 1967). When Done and Heatwole (1977) treated subordinate male skinks with testosterone, the individuals increased their aggressive levels and consequently improved their social status in a social hierarchy. Unfortunately, there have been few studies showing the relationship between aggression and home range development in juvenile lizards (but see Stamps, 1978). Other studies on the relationship

between aggression and home range quality are needed. There is indirect evidence that more aggressive Sceloporus undulatus have a better chance of survival when some resources in the habitat are limiting (Tubbs and Ferguson, 1976; Ferguson and Bohlen, 1978; Ferguson, Hughes, and Brown, 1980).

Home Range Ecology

A puzzling aspect of this study is the sham control pairs. Those individuals with initially superior HRQ scores displayed a significant decline in their home range qualities when exposed to a novel habitat, whereas their pair-mates (those with originally low HRQ scores) subsequently rose. One would expect the initially high HRQ individuals to reacquire superior home ranges when placed in new habitat if those lizards still displayed characteristics that enhanced the procurement of superior home ranges. Under the null hypothesis, though, lizard characteristics should not affect home range acquisition. One would expect the mean of the high quality group would rise, and that of the low HRQ group would fall, since each was a non-random group of pre-selected HRQ extremes; the two groups would converge to a common index of HRQ. The final HRQ scores of the two control groups were in fact not different (Mann-Whitney U test, $p > .05$). This apparent convergence of home range qualities may have resulted from an abundance of sometimes limiting environmental resources at the time the study was conducted. If this were the case, then one should expect minimal aggression since there would be lax competition

between lizards over home ranges of different features; fitness may have been unrelated to home range features at the time the study was conducted.

If there was an abundance of otherwise limiting environmental resources the year of the study, why did the testosterone implants increase the quality of their home ranges at a time when HRQ was comparatively unrelated to survival? Normally the lizards are in competition over limiting environmental resources. More aggressive juveniles will be favored through interference competition (Fox, 1980). The more aggressive individuals will come to inhabit home ranges with more of the limiting resources. But only when these resources are limiting would there be an adaptive advantage in aggressively securing "better" home ranges. In this experiment, lizards were made artificially more aggressive independent of the environmental resource level. The testosterone implants acquired habitat characteristics which were not highly correlated with survival that year. Resources were probably not greatly limiting the year this study was conducted. The increased level of aggression the testosterone lizards displayed may very well have been of questionable benefit that year, even though it would generally be adaptive in a more competitive year.

In summary, the elevation of aggressive levels via testosterone implants aids juvenile Uta in the acquisition of larger and superior home ranges when they are placed in a novel habitat. This does not, however, show conclusively

that aggression is the sole causal agent in determining territorial quality among natural populations. The aggressive level of an individual may be influenced by a number of factors, both internal and environmental. Additional research is needed to test how important early habitat experience is to the subsequent level of expressed aggression and to what degree aggression serves to promote superior home range acquisition in environments that show temporal variation in the importance of home range features.

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