

AN ABSTRACT OF THE THESIS OF

Edith Moore for the degree of Master of Science
in Zoology presented on August 16, 1983
Title: The Function of Orange Breeding Coloration in the Social
Behavior of the Long-nosed Leopard Lizard (Gambelia wislizenii)
Abstract approved: Redacted for Privacy
Dr. Robert M. Storm

The role of orange coloration in the breeding behavior of Gambelia wislizenii was examined in the Alvord Basin of southeast Oregon. Behavioral observations of free ranging lizards supplemented field experiments where I manipulated the sex and color of lizards encountered by resident female G. wislizenii before and after they acquired orange coloration. G. wislizenii exhibited a behavioral repertoire typical of the family Iguanidae. Twenty-four behaviors were observed and discussed in the text.

Female G. wislizenii avoided plain females and males early in the breeding season, while males courted both indiscriminately. Female avoidance forced males to pursue females in order to secure the neck grip necessary for copulation. Female coyness may exert selective pressure on males to display characteristics that would improve their offspring's chances of survival. Possible advantages of male-male "courtship" are discussed.

Most orange females were unreceptive to male courtship and reacted with overt aggression to such advances. Males may maintain a neck grip on females for up to three hours, therefore it is to a

gravid female's advantage to discourage male courtship, and thus avoid unnecessary incapacitation. The high level aggression of orange females was usually an effective deterrent to male courtship; however, a rape strategy was substituted for courtship on occasion. The rape strategy was characterized by 10-20 m headlong dashes ending in a tackle of the female. This behavior led to wrestling and thrashing, but never to a successful copulation.

Free ranging female-female interactions were rarely observed between plain females but became increasingly frequent between orange females toward the end of the breeding season. Orange females were tolerant of other orange females, but generally intolerant of all plain lizards and became aggressive if approached by a plain lizard of either sex. Orange female tolerance was often preceded by tongue flicking near the vents of other orange females, suggesting that olfactory and/or gustatory cues may be important in sex determination.

Behavioral observations and experimental results indicate that orange coloration in breeding female G. wislizenii serves as a deterrent to male courtship, and as an appeasement signal to other females. It may prevent unnecessary expenditures of energy on the part of males once they learn to associate orange color with unreceptive females, and on the part of females which need not display high level aggressive postures toward other females to discourage courtship. Deterrence of courtship may be important in protecting gravid females from excessive exposure to predation, and interruption of feeding.

The Function of Orange Breeding Coloration in the Social
Behavior of the Long-nosed Leopard Lizard (Gambelia wislizenii).

by

Edith Moore

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirements for the

degree of

Master of Science

Completed August 16, 1983

Commencement June 1984

APPROVED:

Redacted for Privacy

Professor of Zoology in charge of major

Redacted for Privacy

Chairman, Department of Zoology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented: August 16, 1983

Typed by Suzi Sargent for: Edith Moore

ACKNOWLEDGEMENTS

Throughout the course of this study, and during manuscript preparation, many people provided logistical support and professional advice. For all those not specifically named, your help was greatly appreciated.

I would like to thank Dr. Storm, my major professor, for both moral support and practical advice throughout my study in addition to editing of the manuscript. Dr. Andrew Blaustein commented on experimental design and was of great assistance in editing the manuscript. My officemate Diana Hews was a constant source of ideas and enthusiasm in those dark hours of doubt. I extend special thanks to all the people of Fields, Oregon who accepted us into their community and made us feel at home in the desert. Technical assistance was provided by Suzi Sargent who typed the manuscript, and Suzie Maresch who provided statistical consultation. I am especially grateful to Susan Lindstrom who took time out from her research to hand paint my models and wanted only pencils in return.

I would like to thank my family who has always supported my various endeavors regardless of whether they understood them or not. Most of all I owe my deepest thanks to Marc Liverman who was not only my field assistant throughout the entire study, but who provided valuable input on experimental design, and plant sampling techniques. Marc made life in the desert a joy; his hard work and high spirits stimulated my work from start to finish.

Research funding was provided by Sigma Xi, the OSU Department of Zoology, and the OSU Computer Center.

TABLE OF CONTENTS

	<u>Page</u>
I. INTRODUCTION.....	1
II. DESCRIPTION OF THE STUDY AREA.....	4
Site Selection and Location.....	4
Geology.....	4
Climate.....	7
Plant Composition.....	8
Vertebrates.....	13
III. MATERIALS AND METHODS.....	15
Determination of Home Range.....	15
Intensive Observations of Individuals.....	17
Experimental Manipulations.....	18
IV. RESULTS.....	21
General Activity Patterns.....	21
Size Distribution and Growth.....	22
Home Range Size.....	25
Density.....	25
Foraging Behavior.....	33
Social Behavior.....	34
Miscellaneous Behavior.....	37
Experiments.....	38
V. DISCUSSION.....	49
General Activity Patterns.....	49
Size and Growth Rate.....	51
Home Range Size.....	52
Density.....	55
Foraging Behavior.....	57
Social Behavior.....	59
Male-Male Interactions.....	61
Courtship Behavior.....	62
Female-Female Interactions.....	65
Miscellaneous Behaviors.....	65
Role of Orange Coloration in Social Behavior.....	67
General Discussion.....	68
Conclusions.....	71
VI. LITERATURE CITED.....	72
VII. APPENDICES.....	79

LIST OF FIGURES

<u>Figure No.</u>		<u>Page</u>
1	Distribution of <u>Gambelia wislizenii</u>	5
2	Location of study area.....	6
3	Frequency distribution of length/weight ratio for male and female <u>G. wislizenii</u>	24
4	Home range areas for 38 females mapped within the study area.....	27
5	Home range areas for 38 males mapped within the study area.....	28
6	Observed density of male and female <u>Gambelia wislizenii</u> throughout the study period.....	30
7	Number of captures and recaptures of <u>Gambelia wislizenii</u> throughout the study period.....	32
8	Behavioral repertoire of <u>Gambelia wislizenii</u>	35

LIST OF TABLES

<u>Table No.</u>		<u>Page</u>
1	Comparative 1982 climatological data.....	9
2	Shrub species arranged by cover importance.....	10
3	Substrate types arranged by cover importance.....	11
4	List of non-shrub plant species.....	12
5	Vertebrates sighted with the study area.....	14
6	Home range areas in hectares ordered by sex and the number of sightings used to determine them.....	26
7a	Summary of reactions of plain resident females to the introduction of plain females, plain males, and orange females.....	39
7b	Summary of reactions of orange resident females to the introduction of plain females, and orange females.....	39
8	Tabulation of behaviors observed between plain resident females, plain females, plain males and orange females.....	40
9	Tabulation of behaviors observed between orange resident females, plain females, plain males and orange females.....	42
10a	Summary of reactions of orange resident females to the introduction of orange females with their orange covered by paint, and to males painted to imitate orange females.....	44
10b	Summary of reactions of orange resident females to the introduction of models painted to imitate plain and orange lizards.....	44
11	Tabulation of behaviors observed between orange resident females, orange females covered by paint and males painted with orange.....	45
12	Tabulation of behaviors observed between orange resident females, plain models and orange models.....	47
13	Comparisons of home range sizes over <u>G. wislizenii</u> distribution.....	53

THE FUNCTION OF ORANGE BREEDING COLORATION IN THE SOCIAL BEHAVIOR
OF THE LONG-NOSED LEOPARD LIZARD (GAMBELIA WISLIZENII)

INTRODUCTION

The role of color in the social behavior of animals has long been a subject of research and speculation. Darwin (1871) first suggested a link between sexually dimorphic coloration and sexual selection. The importance of sexually dimorphic coloration in sex recognition has been demonstrated in birds (Noble, 1936; Selander, 1965), lizards (Noble, 1934; Moseley, 1963; Harris, 1964), and fish (Semler, 1971; Haas, 1976). Intensity and distribution of colors can also serve as a signal of social dominance which may be a strong selective force acting through mate selection. This has been shown in chaffinches (Marler, 1955), sparrows (Rohwer, 1977; Ketterson, 1979), iguanid lizards (Noble & Teale, 1930) and many fish species (McAlister, 1958; Barlow, 1973; Stacey & Chizar, 1977). Color is especially important as a stimulus of social behavior in diurnal lizards (Fitch, 1940; Greenberg, 1945; Ferguson, 1966; Vinegar, 1972).

Fitch (1958) suggests that each lizard family has characteristic behavior patterns that may vary somewhat between genera and species, but are more similar than those seen in other families. The family Iguanidae may depend primarily on visual stimuli such as posturing, pushups, head bobbing, and displays of bright coloration on prominent areas of the body to elicit species specific behavior (Evans, 1961; Brattstrom, 1974). In most iguanid species, males are larger, more

aggressive, and more brightly colored than females (at least during the breeding season). The long-nosed leopard lizard (Gambelia wislizenii) is an exception to this generalization because females are larger than males and it is the female which develops a special breeding coloration, while the male maintains cryptic coloration. Female orange coloration suffuses the undersides of the tail, and appears as spots and bars on the sides of the neck and body (Stebbins, 1966).

Orange coloration appears in female G. wislizenii approximately at the time of ovulation (Tanner & Krogh, 1974a). Stejneger (1893) found that females displaying this coloration contained eggs 12-15 mm long with the coriaceous shell already formed, and thus described the coloration as a post-copulatory phenomenon. Turner et al. (1969) found that females containing follicles at least 12 mm long or ovulated eggs, developed orange coloration. Some authors have suggested that the orange coloration of female G. wislizenii functions to discourage males from copulation (Carpenter, 1967; Fitch, 1967), while others have suggested that it may attract males by advertising the reproductive condition of females (Tollestrup, 1972; Medica et al., 1973). Abts (1976) suggested that the coloration might be an aggressive signal between females which would provide a spacing mechanism ensuring adequate room for each female to lay eggs without the danger of other females accidentally digging up their eggs.

The general ecology of G. wislizenii has been studied throughout their range (Pack, 1922; Tinkle, 1959; Woodbury, 1959; Banta, 1962;

Jorgensen et al., 1963; Wever et al., 1966; McCoy, 1967; Montanucci, 1967; Turner et al., 1969; Snyder, 1972; Tollestrup, 1972; Medica et al., 1973; Clark, 1974; Tanner & Krogh, 1974a, b; Abts, 1976; Parker & Pianka, 1976; Pietruszka et al., 1981; Whitaker & Maser, 1981).

Though a number of these studies discuss the behavior of G. wislizenii, the information provided is largely anecdotal. There has been no study to date which examines the structure of their social system, or the role of orange female coloration in breeding behavior.

The purpose of this study was to examine the role of orange coloration in the breeding behavior of G. wislizenii, and to relate breeding behavior to the social structure of southeastern Oregon populations. I studied the behavior of free-ranging individuals of both sexes, and then compared these observations with experiments conducted in the field, where I manipulated the sex and color of lizards encountered by resident female G. wislizenii within their normal areas of activity. In this way, I hoped to test the hypothesis that orange coloration functions as a spacing mechanism which prevents extensive overlap of female activity areas during the breeding season. Experiments were designed to test the effect of female coloration on the mating behavior of male G. wislizenii.

DESCRIPTION OF THE STUDY AREA

Site Selection and Location

G. wislizenii is a common species of brushy desert flats throughout the Great Basin (Stejneger, 1893; Taylor, 1912). Generally avoiding dense vegetation, they may be found on a variety of soil types (Brooking, 1934; Tinkle, 1959; Stebbins, 1966) (Fig. 1). The study site was located in the Alvord Basin of southeastern Oregon (R35E, T33S, NW 1/4 section 13, Harney County) (Fig. 2). The grid was 300 m x 300 m (9 hectares) and subdivided by stakes 20 m apart. A 60 m buffer zone surrounded the entire grid. The study location was selected for two reasons: 1) it provided a large area of suitable habitat for G. wislizenii, and 2) it is fairly remote and receives little human disturbance.

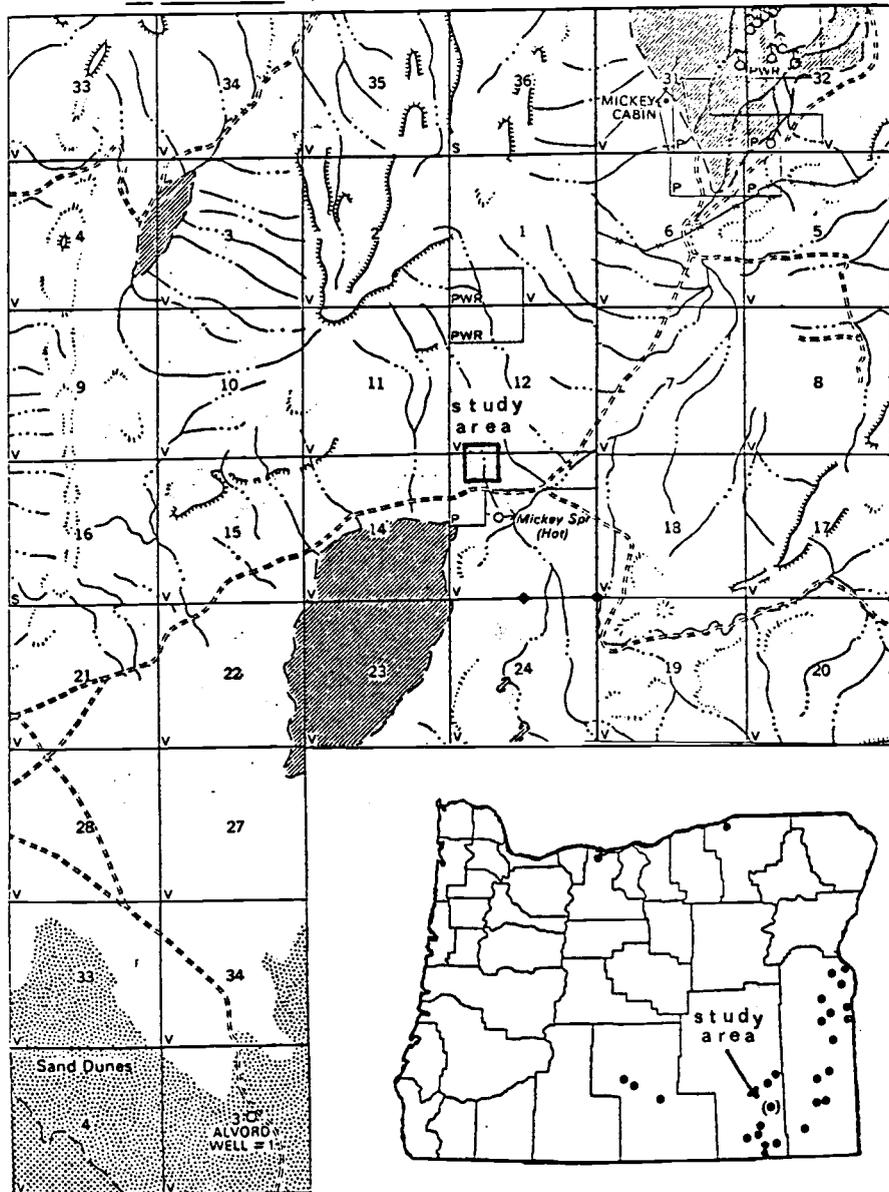
Geology

The Alvord Basin is the most easterly of seven major structural depressions in Oregon's Basin and Range province (Walker, 1969). The basin is long and narrow, bound on the west by the massive fault scarps of Steen's and Pueblo mountains, and on the east by the Sheepshead and Trout Creek mountains. Its southern limit extends into the Quinn River Valley of Northern Nevada; to the north it gradually rises and merges with the Owyhee Upland province. Basin

Fig 1. Distribution of Gambelia wislizenii



Figure 2. Location of the study area. Inset, Oregon distribution of *Gambelia wislizenii* (Nussbaum, Brodie & Storm, 1983).



floor elevations range from 1200 m - 1400 m, and the highest surrounding point is Steen's Mountain, over 2900 m.

The following geologic information was taken from McKee (1976). The structural patterns of the Alvord Basin resulted from a combination of faulting and volcanic activities. Volcanic strata are imbedded with non-marine sandstone, shale, and conglomerate beds. Heavy precipitation during the Pleistocene glacial periods created pluvial lakes which at peak volume covered the basin floor. Prominent shoreline features are still visible on many of the lower basin walls. Today, the basin floor is generally flat and composed of sediments deposited in the ancient lakes, as well as alluvium from surrounding highlands. Isolated playas, alkaline lakes, cold and hot springs, and sand dunes are characteristic landform features.

Climate

The Alvord Basin is a cold desert. Annual temperatures at Andrews, Oregon average 9.4°C and range from -7.6°C to 33.3°C (Johnsgard, 1963). High elevation and low humidity favor strong daytime heating and strong radiational cooling at night. Daily temperatures can span over 22°C. Annual precipitation occurs primarily as snowfall and rain during winter and spring storms. Summer weather is mostly fair and sunny. Cloudless days are commonly accompanied by dry, hot, mid-day winds that blow mixtures of dust and sand high into the air.

Table 1 gives the mean monthly temperatures and precipitation for the Alvord Basin in 1982 as compared with the 20-year mean. The overall climate in 1982 was somewhat colder and wetter than normal, but the only large deviation was the rainfall received in July.

Plant Composition

Vegetation of the study area is transitional between the shadscale and sagebrush zones described by Holmgren (1972). Physiognomically, it can be described as a shrub-steppe community with an open aspect, small shrubs (0.2 - 1 m tall), and a scattering of perennial and annual grasses and forbs.

Plant community composition, structure, and substrate characteristics were examined using a combination of point-centered quarter and canopy coverage techniques (Mueller-Dombois & Ellenberg, 1974; Daubenmire, 1959). Both methods were applied to a randomly selected sample of 100 points located within the study area.

Table 2 lists the shrub species in order of cover importance. Substrate types found between shrubs are listed by cover importance in Table 3. Greasewood (Sarcobatus vermiculatus), bud sage (Artemisia spinescens), catsclaw horsebrush (Tetradymia spinosa), and slender bush buckwheat (Eriogonum microthecum) were also observed within the study area in amounts which proved to be analytically undetectable at this sample size. Non-shrub plant species identified within the study area are listed in Table 4.

Month	Mean Temperature (°F)			Monthly Precipitation (in.)		
	Andrews-Weston Mine	South-Central Oregon Division	Departure From Normal	Andrews-Weston Mine	South-Central Oregon Division	Departure From Normal
JAN	29.4	26.8	-2.1	1.17	1.09	-.54
FEB	33.1	32.5	-1.7	1.02	1.28	.19
MAR	38.2	37.6	0	1.28	1.07	.14
APR	43.0	40.8	-3.4	.49	.79	.05
MAY	53.4	50.3	-1.1	.40	.60	-.74
JUN	63.2	59.8	1.9	1.13	1.64	.36
JUL	70.2	64.2	-1.5	1.31	2.07	1.53
AUG	72.0	65.3	1.6	.11	.51	.05

Table 1. Comparative 1982 climatological data for the Alvord Basin (Andrews-Weston Mine) and South-Central Oregon Climatological Division. Departure from Division normal calculated using standard twenty-year mean.

SPECIES	Canopy Cover per 100m ²	# Shrubs per 100m ²	Mean Shrub height (m)	Mean Shrub cover (m ²)
Big sage (<u>Artimisia tridentata</u>)	15.63	20.3	.77	.59
Littleleaf Horsebrush (<u>Tetradymia glabrata</u>)	4.16	4.0	1.04	.55
Saltbush (<u>Atriplex confertifolia</u>)	1.39	4.2	.33	.35
Spiny Hopsage (<u>Atriplex spinosa</u>)	1.31	1.8	.73	.53
Grey Rabbitbrush (<u>Chrysothamnus nauseosus</u>)	.70	1.8	.39	.35
Green Rabbitbrush (<u>Chrysothamnus viscidiflorus</u>)	<u>.49</u>	<u>1.3</u>	.38	.39
TOTAL=	23.68	33.4		

Table 2. Shrub species arranged by cover importance.

Substrate Type	Area Covered per 100 m ²	% Non-shrub Cover
Loose Sand & Fine Gravel	55.64	72.9
Plant Litter	6.64	8.7
Consolidated Sand	6.18	8.1
Grasses	5.80	7.6
Rock	.99	1.3
Herbs & Moss	.61	.8
Bedrock	<u>.46</u>	<u>.6</u>
TOTAL=	76.36	100.0

Table 3. Substrate types arranged by cover importance.

<u>Boraginaceae:</u>	
<u>Cryptantha circumscissa</u> (matted cryptantha)	<u>Cryptantha nubigena</u> (Sierra forget-me-not)
<u>Coldenia nuttalli</u> (Nuttall's coldenia)	<u>Amsinkia tessellata</u> (tesselate fiddleneck)
<u>Capparidaceae:</u>	
<u>Cleome lutea</u> (yellow spider flower)	
<u>Compositae:</u>	
<u>Chaenactis douglasii</u> (false yarrow)	<u>Layia glandulosa</u> (white daisy tidytips)
<u>Lygodesmia spinosa</u> (spiny skeleton weed)	<u>Lygodesmia</u> sp.
<u>Cruciferae:</u>	
<u>Thelypodium lacinatum</u> (thick-leaved thelypody)	<u>Descurainia sophia</u> (tansy mustard)
<u>Lepidium perfoliatum</u> (clasping peppergrass)	
<u>Gramineae:</u>	
<u>Hordeum jubatum</u> (foxtail barley)	<u>Stipa comata</u> (needle & thread grass)
<u>Distichlis stricta</u> (saltgrass)	<u>Dryzopsis hymenoides</u> (Indian ricegrass)
<u>Bromus tectorum</u> (cheat grass)	
<u>Leguminosae:</u>	
<u>Astragalus lentiginosus</u> (freckle-pod milk vetch)	<u>Astragalus</u> sp.
<u>Astragalus speirocarpus</u> (curve-pod milk vetch)	<u>Astragalus malcus</u> (shaggy milk vetch)
<u>Lupinus pusillus</u> (low lupine)	
<u>Liliaceae:</u>	
<u>Allium nevadense</u> (Nevada onion)	<u>Leucocrinum montanum</u> (sand lilly)
<u>Calochortus</u> sp. (Mariposa lilly)	
<u>Loasaceae:</u>	
<u>Mentzelia albicaulis</u> (small flower blazing star) <u>Mentzelia laevicaulis</u> (blazing star)	
<u>Onagraceae:</u>	
<u>Oenothera boothii</u> (alyssum-like evening primrose)	
<u>Oenothera claviformis</u> (club-fruit evening primrose)	
<u>Oenothera caespitosa</u> (desert evening primrose)	
<u>Oenothera deltoides</u> (hairy evening primrose)	
<u>Orobanchaceae:</u>	
<u>Orobanche fasciculata</u> (clustered broomrape)	
<u>Polemoniaceae:</u>	
<u>Gilia sinuata</u> (shy gilia)	<u>Leptodactylon pungens</u> (prickly phlox)
<u>Polygonaceae:</u>	
<u>Eriogonum chryseps</u> (golden buckwheat)	
<u>Ranunculaceae:</u>	
<u>Delphinium andersonii</u> (desert larkspur)	
<u>Scrophulariaceae:</u>	
<u>Castilleja</u> sp. (Indian paint brush)	<u>Penstemon speciosus</u> (showy penstemon)
<u>Penstemon acuminatus</u> (sand-dune penstemon)	
<u>Umbelliferae:</u>	
<u>Rhysopterus plurijugus</u> (wrinkled wing)	

Table 4. List of non-shrub plant species.

Vertebrates

G. wislizenii was rarely observed to interact with other lizard species. However, Uta stansburiana was common in the study area before Gambelia emergence, and later was largely restricted to rocky crevices, suggesting that there might be some predation pressure from Gambelia. No predation attempts were observed. On occasion Cnemidophorus tigris appeared agitated in the presence of a G. wislizenii, but more commonly they would ignore one another.

Predators observed to prey on G. wislizenii included the striped whipsnake (Masticophis taeniatus), American kestrel (Falco sparverius), sharp-skinned hawk (Accipiter striatus), and loggerhead shrike (Lanius ludovicianus). Other possible predators include the gopher snake (Pituophis melanoleucus), W. rattlesnake (Crotalus viridis), coyote (Canis latrans), and Red-tailed hawk (Buteo jamaicensis).

All vertebrates sighted within the study area are listed in Table 5.

I Reptiles:

Gambelia wislizenii (long-nosed leopard lizard)
Phrynosoma platyrhinos (desert horned lizard)
Masticophis taeniatus (striped whipsnake)
Crotalus viridis (western rattlesnake)

Uta stansburiana (side-blotched lizard)
Cnemidophorus tigris (western whiptail)
Pituophis melanoleucus (gopher snake)

II Mammals:

Taxidea taxus (badger)
Anospermophilus leucurus (antelope ground squirrel)
Dipodomys ordii (ord kangaroo rat)
Lepus californicus (blacktail jackrabbit)
Sylvilagus idahoensis (pygmy rabbit)

Canis latrans (coyote)
Perognathus parvus (Great Basin pocket mouse)
Peromyscus maniculatus (deer mouse)
Sylvilagus nuttalli (mountain cottontail)
Antilocapra americana (pronghorn)

III Birds:

Cathartes aura (turkey vulture)
Buteo jamaicensis (red-tailed hawk)
Athene cunicularia (burrowing owl)
Oreoscoptes montanus (sage thrasher)
Sturnella neglecta (western meadowlark)
Amphispiza bilineata (black-throated sparrow)
Spizella breweri (Brewer's sparrow)

Accipiter striatus (sharp-shinned hawk)
Falco sparverius (American kestrel)
Chordeiles minor (common night hawk)
Lanius ludovicianus (loggerhead shrike)
Chondestes grammacus (lark sparrow)
Amphispiza belli (sage sparrow)
Zonotrichia leucophrys (white-crowned sparrow)

Table 5. Vertebrates sighted within the study area.

MATERIALS AND METHODS

Data collection was divided into three parts: 1) determination of home range, 2) intensive observation of individuals, and 3) experimental manipulation. All work was conducted between 8 May and 12 July, 1982. During this period the study area was monitored four days a week for four hours in the morning and three hours in the afternoon, as weather permitted, for a total of 273 hours.

Study dates were chosen to include emergence and peak mating so that the home ranges of females could be mapped and experiments completed before egg laying began (2-1/2 months) (McCoy, 1967; Abts, 1976). Abts (1976) found that emergence of G. wislizenii in the Alvord Basin occurred between late April and early May. During 1982 emergence, as determined by frequent preliminary visits to the study area, occurred during the last week of April, although isolated individuals were seen as early as April 16.

Determination of Home Range

All G. wislizenii encountered within the nine hectare boundary zone were noosed and toe clipped for permanent identification. Toe clipping involved only two toes, and never from the same foot. Toe clip formulas were painted on their backs with flat, white, acrylic paint that quickly became dusted and blended well with the animal's ground color. Males and females were marked with numbers ranging from 1-49 and 50-100, respectively. Additional lizards encountered

toward the end of the study were marked with an F (female) or M (male), and a number, but were not toe clipped. Numbers facilitated the identification of individuals and sex from a distance using 7 x 35 binoculars, without interfering with their activities. The paint persisted on most individuals until they shed in late June or early July but was easily replaced by reading the permanent toe clip formula. In addition, when first captured, each animal was weighed to the nearest 0.5 gm, and measured to the nearest 1 mm (snout-vent length).

Each time a lizard was seen, its location was recorded on a coordinate system that divided each 20 m square into sixteen 5 m squares. This system imposes an accuracy limit of ± 2.5 m; however, considering the highly mobile nature of this species, I thought that a finer grained estimation would be unnecessary. At the end of each day, locations were mapped for each individual.

The grid was observed daily by myself and my field assistant. We walked down each row 5 m from the stakes, and 10 m from each other, so that each observer was responsible for 5 m on either side of them. The order in which the rows were walked was shifted daily so that no bias due to time of day and specific locations was introduced. We found that working as a team, one observer might locate a lizard which their partner had startled. When startled, lizards generally ran only a few meters before freezing, frequently at the edge of a shrub, so that we could identify them without further disturbance.

Home range was determined by the minimum polygon method. Since Burt (1943) defined the term home range, numerous methods have been developed to determine home range (Hayne, 1949; Calhoun & Casby, 1958; Tinkle et al., 1962; Jorgensen & Tanner, 1963; Tinkle, 1967; Jennrich & Turner, 1969; Turner, 1971). Milstead (1972) reviewed these methods and pointed out that each was biased according to primary assumptions regarding the shape of home ranges, or suitability of habitat within drawn home range boundaries. I have chosen the minimum polygon method for two reasons: 1) It has been used historically in studies of G. wislizenii and is therefore comparable with other literature, and 2) It may more accurately show home range boundaries which would be important if agonistic behavior plays a role in the spacing of individuals.

Density was determined by identifying the point on a graph of new captures versus recaptures where new captures declined markedly, and counting the number of lizards marked before this date. Lizards marked after this date were considered immigrants. The nomadic behavior of this species makes an accurate determination of density difficult. By attempting to eliminate immigrants, I hoped to avoid overestimating density.

Intensive Observations of Individuals

Though behavioral observations were made throughout the study, discrete periods were set aside for intensive observations of individuals. The observer walked within the grid area until a lizard

was located, and then backed away as far as possible while still being able to watch the animal through binoculars. Once the observer ceased moving, the animal became oblivious to their presence and continued to bask, feed, or court. Observation periods lasted for two to three hours unless the lizard retreated into a burrow. Lizards remaining in fully-excavated burrows for longer than 15 min. normally closed off the opening with soil, at which time we terminated the observation. Observations of free-ranging lizards were critical to the interpretation of behavior observed in experiments. We were able to observe encounters with other species as well as encounters with conspecifics.

Experimental Manipulations

Once the home ranges of resident females were determined, lizards from outside the study area were introduced to resident females in their normal areas of activity as follows: 1) an orange female, 2) a non-orange female, 3) a male, 4) a male painted with orange, 5) a non-orange female painted with orange, 6) an orange female with her orange painted over, 7) models painted with orange, 8) models without orange. Plain males, females, and models were painted with orange acrylic paint on the entire undersides of the tail, two rows of spots on the sides of the body, and small blotches along the jaw, as seen in resident orange females. Orange females were painted with flat white acrylic on the undersides of the tail, and with brown acrylic on their sides and face to cover up all orange pigment. The use of

these two colors resembled the natural colors of non-orange females, especially once they had become dusted. Models were made from plaster casts of museum specimens, and cast with RTV standard moulding rubber. This compound is strong but flexible and lifelike when moved. Models were handpainted to resemble plain and orange colorations exhibited by southeastern Oregon G. wislizenii.

Experiments were generally conducted on both plain and orange resident females; however, not all were completed on plain resident females because of the difficulty of locating both plain and orange females outside the study area at the same time. Once females began to turn orange, we had very little time before all had become orange (May 30 - June 25). We had not determined enough resident female home ranges to begin experiments until June 14.

Each experiment was repeated six times; with three repetitions in the morning, and three in the afternoon. Experimental lizards were taken from outside the study area. Difficulties in obtaining an adequate supply of experimental lizards required that some be used in up to three repetitions. It is possible that learning occurred which could bias experimental results. However, resting periods of from .5 to 2 hours between repetitions may have reduced this effect. If lizards the size of residents were not used, an equal number of experimental lizards which were larger, and smaller than the residents were used whenever possible. For experiments, the introduced lizards were suspended with monofilament line from a 1 m fly rod and noose, and released approximately .5 m from the resident female. If the resident reacted with avoidance to the introduction

procedure, the lizard was retrieved and the process begun again from a new position. Normally only one or two trials were necessary to successfully introduce experimental lizards. If the third attempt was not successful, a different resident and experimental lizard were chosen. Before we developed this method, we attempted to run experiments by enclosing the two lizards in a 5 m diameter arena made of .5 m wide sheet metal stripping which was painted gray and placed within the resident's activity area. This method proved ineffective because both lizards ran to the sides of the enclosure immediately and sought escape.

Once both lizards were in place and aware of each other's presence, the experiment began, and detailed observations were made on the behavior and orientation of both lizards. Experiments lasted until the pair voluntarily moved more than 5 m apart. Time periods varied from 1-23 min. depending on the level of tolerance displayed by the lizards involved. Models were introduced on the end of a 1 m long line of monofilament so that they could be manipulated without disturbing the resident female. Models were manipulated to mimic behaviors typically displayed by males and orange females.

RESULTS

General Activity Patterns

G. wislizenii were active in the study area between 0700 and 1800, but were present in the greatest numbers at mid-morning and late afternoon. Males were likely to be sighted several days in a row, often covering a great deal of territory between sightings. Females tended to be seen for a day or two and then to disappear for a week or more, often to reappear very close to their last known location. This sexually dimorphic activity pattern gives the illusion of an unequal sex ratio. However, the sex ratio is even, as determined by the total number of males and females marked.

On several occasions (June 10, 25, and 27) females were observed excavating and retreating into burrows. Burrows consisted of simple tunnels about 7 cm deep and running 20-30 cm parallel to the surface, and terminating in a chamber large enough for one adult to turn around. Once a burrow was complete, the lizard retreated into it and blocked off the opening with soil. Closed burrows were difficult to locate even after we had watched their excavation. We did not observe males excavating burrows, but we did see them retreat into burrows in the late afternoon which were similar to those used by females. The frequency of male observations as compared with female observations suggests that males do not spend as much time estivating as do females.

Adult G. wislizeni did not use burrows of any kind to evade capture. Burrows served as thermoregulatory chambers, and as places to rest for extended periods of time. Speed and agility as well as cryptic coloration were typically employed in predator avoidance. When pursued by the noose, they normally ran short distances and either dove into dense vegetation, or froze at the edge of a shrub where the broken pattern of light and shade blended with the irregular light and dark pattern of their dorsum.

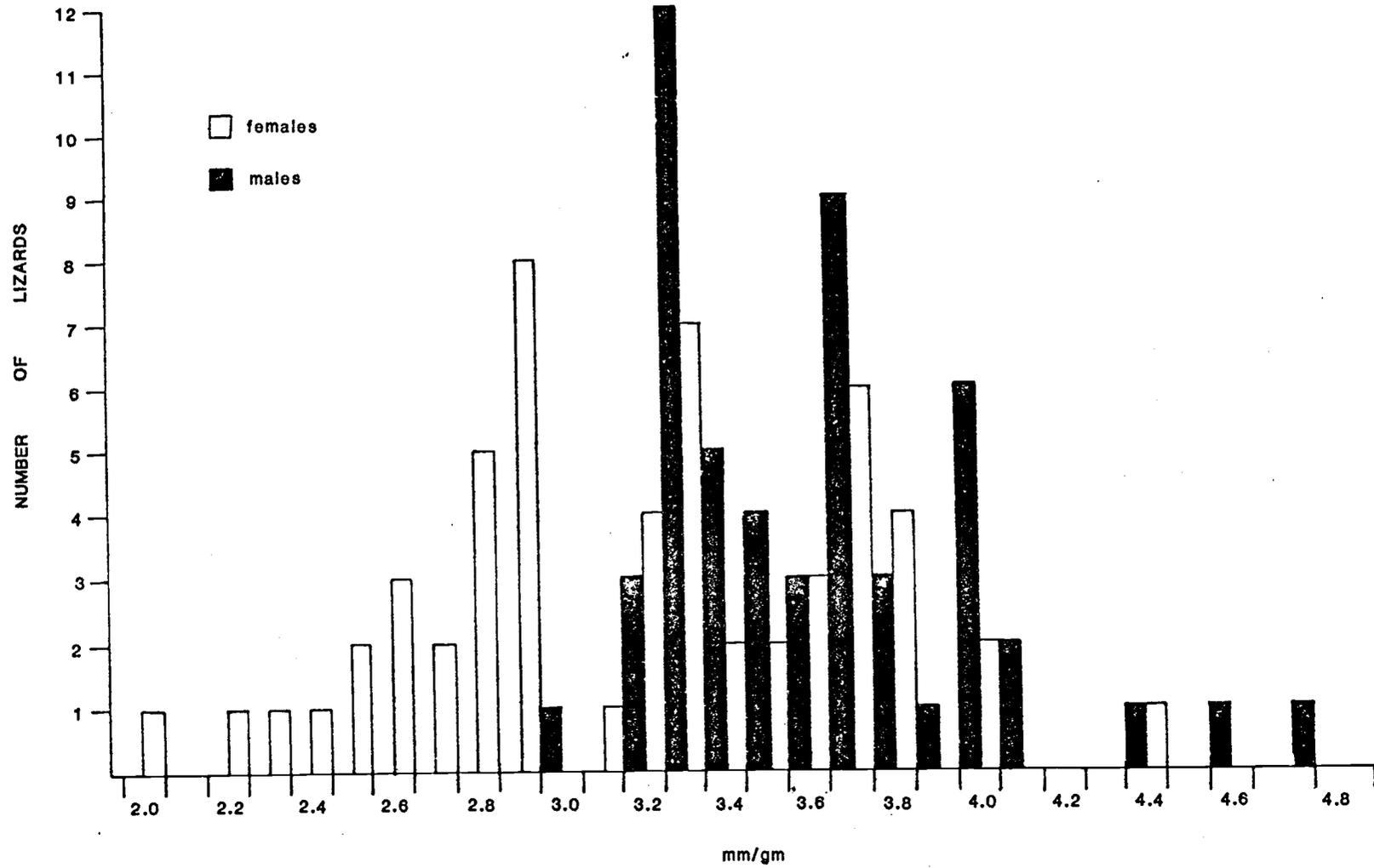
Size Distribution and Growth

Fifty-three adult male G. wislizeni ranged from 77-101 mm (snout-vent length) (\bar{x} = 92 mm; s = 5 mm), and weighed between 17 and 30 gm, (\bar{x} = 25 gm; s = 3 gm). 55 adult females ranged from 81-115 mm (\bar{x} = 98 mm; s = 7 mm), and weighed between 22 and 53 gm (\bar{x} = 32 gm; s = 7 gm). The two juvenile males we encountered were 67 mm, 6.5 gm, and 68 mm, 8.5 gm. Two juvenile females were 70 mm, 9 gm, and 69 mm, 9.5 gm. Figure 3 shows that males are generally longer than females per unit weight.

The average growth rate for adult females was .10 mm/day and .13 gm/day. Adult males averaged .10 mm/day and .07 gm/day. One juvenile female grew .52 mm/day and .18 gm/day; increasing in length at a rate of more than five times that of an adult female. One juvenile male grew .37 mm/day and .29 gm/day, showing slower growth in length than female juveniles, but nearly four times the growth of adult males. The male juvenile increased in weight four times the

Figure 3. Frequency distribution of length/weight ration for male and female Gambelia wislizenii.

Figure 3.



rate of an adult male; the female juvenile increased in weight at a rate close to that of adult females.

Home Range Size

Home range areas were determined for 35 females, 36 males, and four juveniles. Female home ranges varied from .001-1.66 hectares (ha) (\bar{x} = .36 ha; s = .43 ha). Male home ranges were between .004 and 2.80 ha (\bar{x} = .62 ha; s = .59 ha.). Juvenile home ranges were between .12 and .21 ha. Table 6 gives home range areas in hectares, ordered by sex and number of points used to determine them. Home range size and number of points show a significant correlation for males (r = .744; p < .01), but not for females (r = .245; p > .05) or juveniles (r = .632; p > .05).

Density

Spatial and temporal overlap of home range was extensive both intra- and intersexually (Figs. 4 and 5). The degree of overlap was not calculated. Figure 6 shows the number of males and females seen each day. Figure 7 indicates the point where new captures declined used to determine densities as discussed on page 17. Density of G. wislizenii was estimated as 4.67 males and 4.44 females per hectare, for a total of 9.11 per hectare.

NUMBER OF SIGHTINGS								
	3	4	5	6	7	8	9	
♀	.17 (8) .001-1.14	.10 (4) .01-.22	.59 (3) .07-1.34	.47 (7) .04-1.66	.69 (3) .17-1.44	.25 (4) .03-.72	.17 (1)	MEAN RANGE
♂	.05 (4) .004-.08	.26 (5) .06-.79	.29 (4) .13-.42	.34 (3) .18-.53	.39 (2) .24-.54	.38 (1)	1.06 (3) .54-1.92	MEAN RANGE
Juv.	.17 (2) .13-.21			.08 (1)		.12 (1)		MEAN RANGE

Table 6. Home range areas in hectares, ordered by sex and number of sightings used to determine them. The number of lizards included in the mean is given in parenthesis.

NUMBER OF SIGHTINGS								
	10	11	12	13	14	16	18	
♀	.50 (3) .45-.55		.55 (1)		.58 (1)			MEAN RANGE
♂	.81 (3) .39-1.22	.73 (2) .73-.74	.68 (3) .54-.82	.63 (1)	1.05 (2) .92-1.19	2.80 (1)	1.35 (2) 1.32-1.38	MEAN RANGE

Table 6. (cont.)

Figure 4. Home range areas for 38 females mapped within the study area.

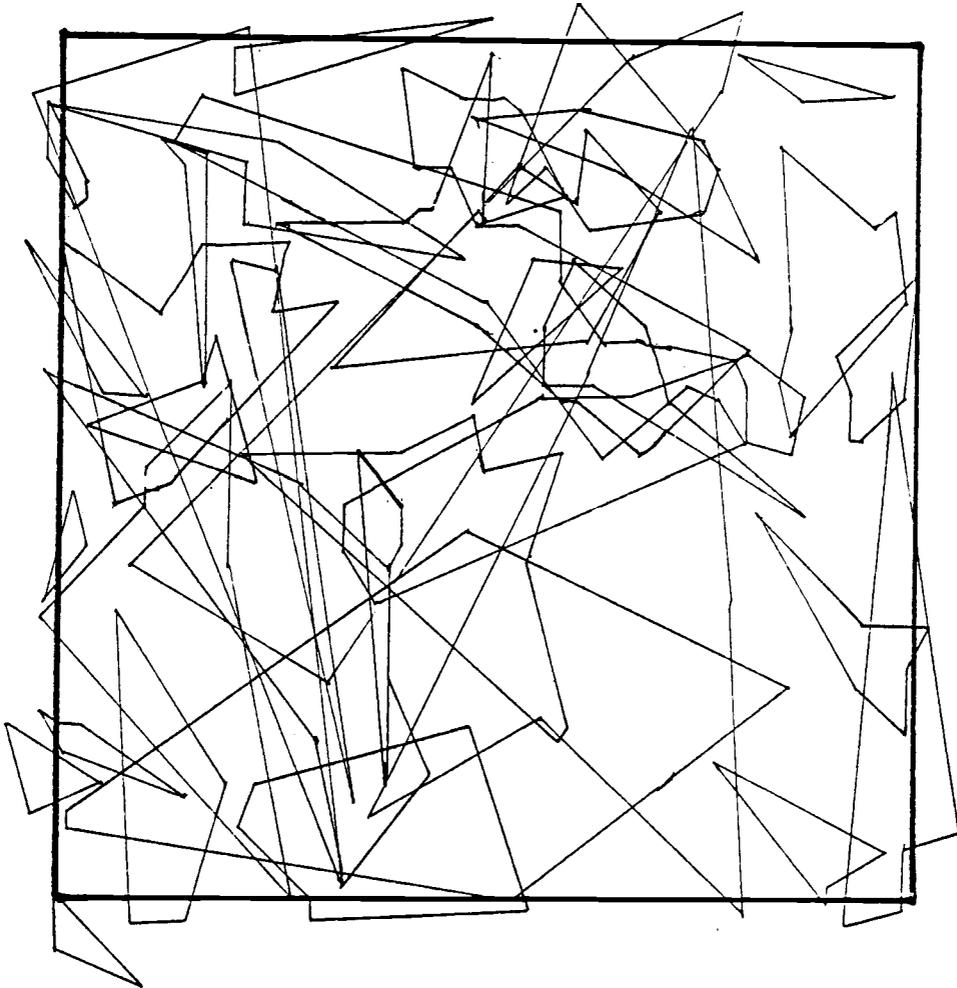


Figure 5. Home range areas for 38 males mapped within the study area.

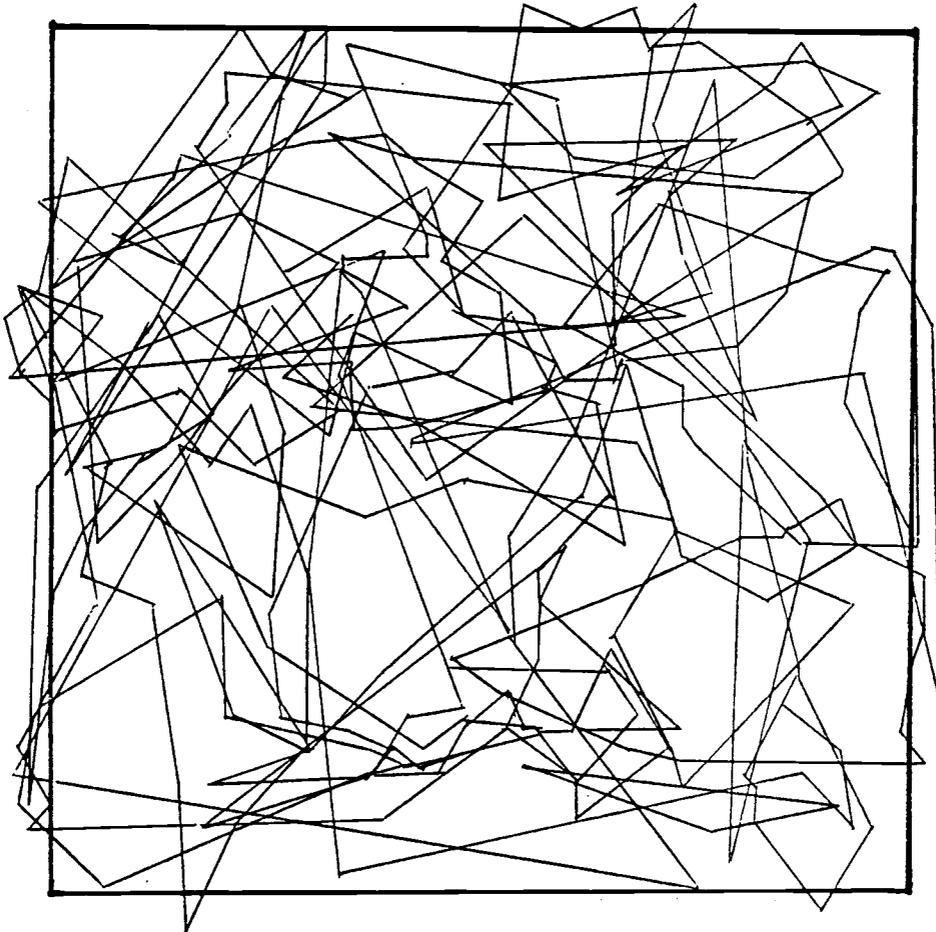


Figure 6. Observed density of male and female Gambeliv wislizeni throughout the study period.

Figure 6.

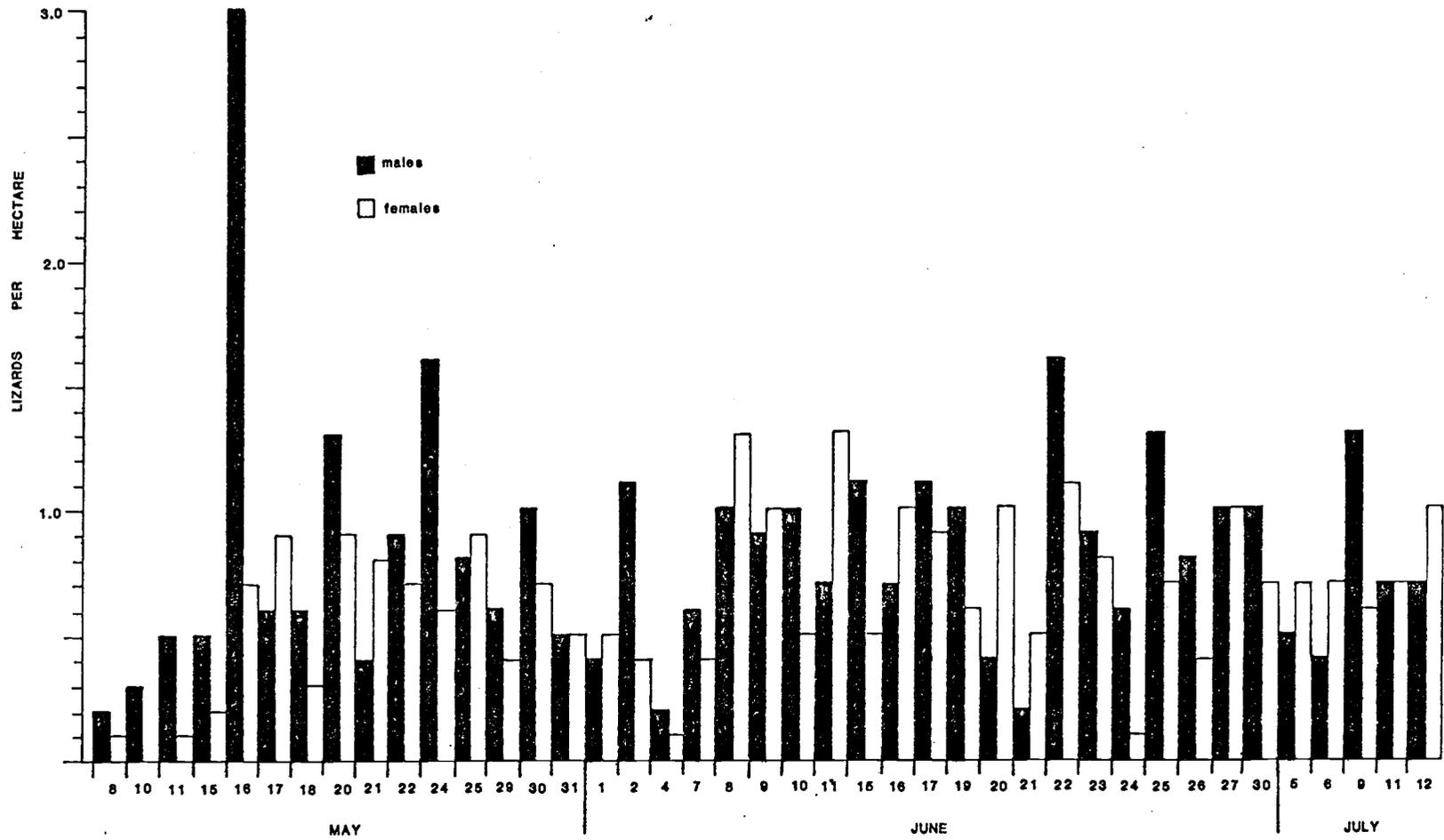
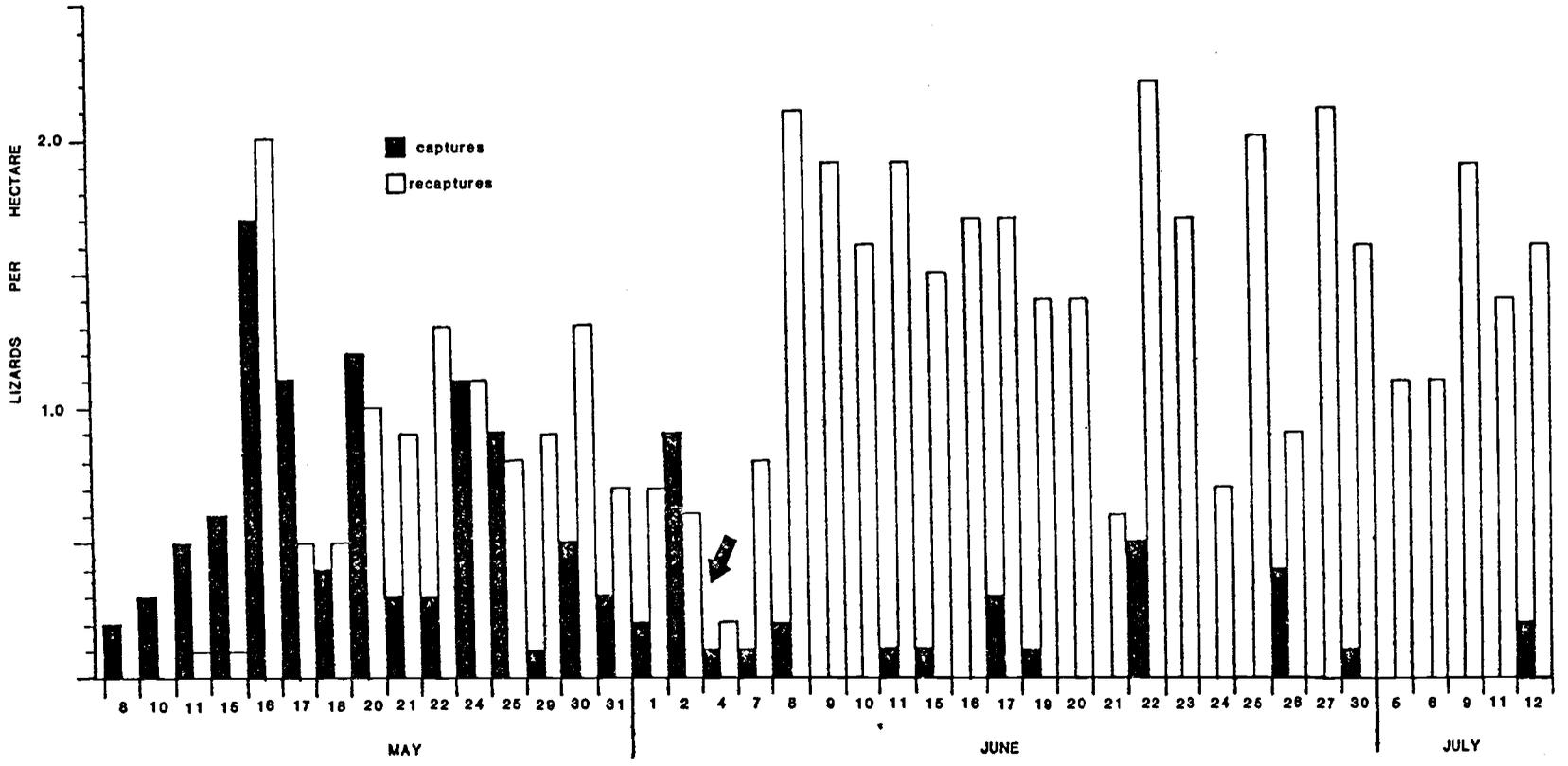


Figure 7. Number of captures and recaptures of Gambelia wislizenii throughout the study period. The arrow indicates the point of inflection used to determine density in the study area.

Figure 7.



Foraging Behavior

G. wislizenii's usual predatory sequence involves sitting in an inconspicuous place until a prey item is visually located and then carefully stalking the prey in order to get close enough for the final leap. Speed and agility are required for successful predation (this same ability prevented one G. wislizenii we observed from becoming a prey item for Masticophis taeniatus). We observed G. wislizenii to prey on flying insects, particularly cicadas.

On many occasions G. wislizenii was observed to hunt and successfully obtain prey from the top of shrubs. Such scansorial behavior is no doubt adaptive in thermoregulation; however, this behavior was observed on cool days as well as hot days. They often leaped up into shrubs to secure prey items as much as .5 m above the ground.

G. wislizenii did respond to auditory cues such as a cicada buzzing overhead regardless of whether the insect was in view or not. Once visually located, aerial prey were pursued by erratic running and leaping into the air.

We observed a great deal of general tongue flicking (Appendix 1) by individuals of both sexes, but particularly by males. Most general tongue flicking was directed at prominent objects and the entrances of burrows, which suggests that it may play a role in social behavior and/or predator avoidance. Increased general tongue flicking was not observed during foraging.

No interspecific aggression was observed, however, behavior by Uta stansburiana and somewhat by Cnemidophorus tigris suggest that they may occasionally be preyed on by G. wislizenii. Uta were common in the study area prior to G. wislizenii emergence, but after, became largely restricted to rocky crevices. Adult C. tigris and G. wislizenii normally do not respond to one another, but in one encounter, a C. tigris appeared agitated when confronted by a G. wislizenii. A female G. wislizenii had approached a shrub with her head down, and a C. tigris emerged from the shrub and immediately assumed the 4-point position (see Appendix 1), and moved away sideways in an arch until it was 5 m from the G. wislizenii female. The G. wislizenii was attentive, but did not pursue the C. tigris.

Social Behavior

Intensive observations of free ranging G. wislizenii revealed a behavioral repertoire typical of the family Iguanidae (Fig. 8). I identified 24 specific behaviors used in social encounters; behaviors are defined in Appendix 1. Most encounters of G. wislizenii with conspecifics occurred between males and females, or between two males. We rarely found two females in close proximity.

Male behavior when encountering a conspecific was fairly stereotyped regardless of the sex of the individual. The male would approach, tongue flick the air and then attempt to tongue flick the individual, and/or slither over it. This type of behavior elicited a variety of responses depending on the sex and physiological condition

Figure 8. Behavioral repertoire of Gambelia wislizenii.I General Agitation:

pushup → heightened aggression (in presence of another conspecific)
(may be performed alone)

II Exploratory:

approach → general tongue flick → tongue flick at vent (if another
lizard is present)

III Avoidance:

side step → walk away → hop away → leap in the air → run away
bipedal run

IV Aggression:

back arch → turn sideways → sidestep → stiff walk → 4-point position
→ leap in the air → gaping → hissing

V Courtship:

approach → general or vent tongue flick → chin rubbing → straddle
slither
nipping

→ neck grip → copulation

*leg grip → flipping female over (never observed in a successful copulation)

of the recipient. Females before they turned orange (plain females) would respond by moving away a short distance and stopping. This behavior on the part of plain females elicited further courtship behavior from the males such as chin rubbing, slithering, nipping, and other forms of tactile stimulation. If the female responded to these new advances by remaining still, the male then attempted to straddle the female and obtain a neck grip. Females normally hopped away at this point, and courtship continued until the male secured a neck grip, or lost interest. On occasion females which had been abandoned circled around and approached the males, tongue flicking and nudging them. This behavior by females reinitiated courtship, and the process began from the start. Females were observed soliciting only the attention of males which had previously courted them.

Females which had developed their orange coloration, responded to male approach with open aggression and avoidance. Figure 8 gives a typical avoidance sequence. Most males did not pursue courtship with females behaving in this way. Some males adopted a rape strategy toward orange females, and replaced normal courtship with 10-20 m headlong dashes ending in a tackle of the female. These ambushes led to wrestling and thrashing and in all instances observed, the female was able to wrestle free and assume the maximum aggressive posture of 4-point position with gaping and hissing. This behavior was designated as rape because in all cases observed males attempted the neck grip typical of copulation posture, and the females showed high level aggression.

Males encountering other males began courtship behaviors, and did not seem to discriminate between males and plain females. On one occasion when two males met in an open area, they alternately courted one another for approximately 10 minutes before they moved away in opposite directions.

We were able to witness only a few naturally occurring female-female encounters, and of those, only one involved two plain females. Both the plain females were small, and their home range maps indicated that they had adjacent home ranges. Toward the end of the study, we observed orange females in close proximity on several occasions which displayed tolerance toward one another. In one instance, a female climbed over another female to move from the shade into the sun, and the female below did not react at all.

Miscellaneous Behavior

On June 22, a female was observed walking slowly over gravel. She stopped, tongue flicked the ground with her tail arched, and quivered. She then moved her tail to the side and rubbed her cloaca on the substrate before relaxing and moving on. This type of behavior was observed several times and was not accompanied by defecation. It was never performed in the presence of another conspecific.

On one occasion a male was observed courting a female, and another male appeared and ran toward the pair. This caused the first male to leave the area. The intruder tongue flicked the female and

did pushups, but did not court the female. The intruder then approached a rock where the female had first been seen, and after tongue flicking all around it, moved away and left the female alone in the clearing. The original male did not return. This behavior may be an example of "female tending" (an attempt on the part of a male to prevent other males from sexual access to a female). Such behavior was observed only once.

Experiments

Table 7a summarizes the reactions of plain resident females to the introduction of plain females, plain males, and orange females. Plain resident females avoided both plain females and plain males; in 1/2 of the encounters with plain females, the avoidance was mutual. Plain females exhibit both tense tolerance and complete tolerance when reacting with orange females. The distinction between tense and complete tolerance involves a slight flexion of the limbs and raising of the head in response to an introduced lizard versus complete relaxation of the body and a lowered position of the head.

Table 8 presents a complete tabulation of behaviors observed by each member of the experimental pair indicating how many (out of six experiments) each behavior occurred in. The table indicates that males primarily engaged in exploratory and courtship behaviors, while females showed general agitation (pushups) and avoidance as their primary reactions. Twice, plain females ran away in encounters with

REACTION	EXPERIMENTAL MANIPULATION		
	PLAIN ♀ X PLAIN ♀	PLAIN ♀ X PLAIN ♂	PLAIN ♀ X ORANGE ♀
NO REACTION	1	0	0
MUTUAL AVOIDANCE	3	0	0
AVOIDANCE BY RESIDENT	2	6	0
TENSE TOLERANCE	0	0	3
COMPLETE TOLERANCE	0	0	2
# REPETITIONS	6	6	5

Table 7a. Summary of reactions of plain resident females to the introduction of plain females, plain males, and orange females.

REACTION	EXPERIMENTAL MANIPULATION		
	ORANGE ♀ X PLAIN ♀	ORANGE ♀ X PLAIN ♂	ORANGE ♀ X ORANGE ♀
MUTUAL AVOIDANCE	1	0	0
RESIDENT DISPLAYED	5	6	0
TENSE TOLERANCE	0	0	2
INVESTIGATE & TOLERATE	0	0	2
COMPLETE TOLERANCE	0	0	2
# REPETITIONS	6	6	6

Table 7b. Summary of reactions of orange resident females to the introduction of plain females, plain males, and orange females.

	DISPLAY	EXPERIMENTAL MANIPULATION					
		PLAIN ♀ X PLAIN ♀	PLAIN ♀ X PLAIN ♂	PLAIN ♀ X ORANGE ♀			
	PUSHUP	2	2	3			
EXPLORATORY	APPROACH		1	1	4	3	1
	GEN. TONGUE FLICK	1		1	2		2
	VENT TONGUE FLICK			1	2		
AVOIDANCE	HOP AWAY	1	1	6		1	
	RUN AWAY	3		1	1	2	
	BIPEDAL RUN			1			
	4-POINT POSITION			1			1
	GAPING			1			
COURTSHIP	SLITHER				4		
	STRADDLE				1		
	TRY FOR NECK GRIP				2		
	LEG GRIP				1		
	WALK AWAY	3	1	5	3	2	2

Table 8. Tabulation of behaviors observed between plain resident females, plain females, plain males, and orange females. The resident lizard precedes the introduced in each column. The numbers indicate how many of six repetitions each behavior was observed in.

orange females. In both cases these females had previously displayed tense tolerance for several minutes, and I felt that their retreat was more likely a part of continued hunting behavior than avoidance of the introduced lizard. When females hopped away from males they did not go very far, and they continued to react to male movements. When plain females moved away from orange females, they moved to nearby shrubs and resumed thermoregulatory or hunting behaviors.

Table 7b summarizes the reactions of orange resident females to the introduction of plain females, plain males, and orange females. Orange females reacted to plain females and plain males by displaying, rather than by showing avoidance as plain females had in the previous group of experiments. In one experiment an orange female and an introduced plain female showed mutual avoidance. The difference between the reaction of orange females to plain females and plain males was apparently caused by the behavior of the introduced lizard. Orange females displayed to all plain lizards; however, the exploratory and courtship behaviors of plain males elicited aggression from orange females (4-point position and gaping), while the passive response of plain females elicited low aggression and mild intolerance from orange females (Table 9). Orange females showed various levels of tolerance when responding to other females. In two cases they were completely tolerant, in two they were tense but tolerant, and in two they became completely tolerant after tongue flicking one another's vents.

	DISPLAY	EXPERIMENTAL MANIPULATION					
		ORANGE ♀ X PLAIN ♀	ORANGE ♀ X PLAIN ♂	ORANGE ♀ X ORANGE ♀			
	PUSHUP	3	1	6	3		
EXPLORATORY	APPROACH	3	1	1	4	3	2
	GEN. TONGUE FLICK	2	2		2	1	3
	VENT TONGUE FLICK			1	1	3	1
AVOIDANCE	BACK ARCH	4		2			
	TURN SIDEWAYS	2		2			
	SIDESTEP	1		1			
	HOP AWAY			2			
	STIFF WALK	1					
	RUN AWAY	1	1	1		1	
	4-POINT POSITION	1		6			1
	GAPING			2			
COURTSHIP	STRADDLE				1		
	TRY FOR NECK GRIP				2		
	SLITHER				2		
	FLIPPING ♀ OVER				1		
	WALK AWAY	4	2	3	4	5	1

Table 9. Tabulation of behaviors observed between orange resident females, plain females, plain males, and orange females (see Table 8).

Table 9 indicates that orange females react to plain females and plain males with general agitation and avoidance. In the case of plain females, more exploratory behavior is observed, and aggression is almost exclusively reserved for courting males. Orange females reacting with other orange females, exhibit exploratory behavior primarily; in one case low level aggression was observed. Males, as shown earlier, are involved exclusively in exploratory and courtship behaviors.

Table 10a summarizes the reactions of resident orange females to introduced orange females which have been painted to cover their orange, and to males which have been painted to imitate orange females. In 5 repetitions residents responded to painted orange females with agitation, but in 3 of these both females became tolerant after vent tongue flicking. In two cases tense tolerance was maintained, and in one case the females never approached each other, but appeared to be generally tolerant. Residents showed some exploratory behavior with painted males, but five out of six experiments ended in avoidance and aggression due to male courtship attempts. Males were only investigated prior to courtship attempts. In one experiment the male did not court, and the female showed tense tolerance toward him.

Table 11 shows that orange females reacted to painted orange females with general exploratory and low level aggressive behavior, but only once was there a retreat from a painted female. Gaping occurred three times in response to approaches by the introduced

	EXPERIMENTAL MANIPULATION	
	ORANGE ♀ X PAINTED ORANGE ♀	ORANGE ♀ X PAINTED♂
INVESTIGATE & AVOIDANCE	0	2
AVOIDANCE BY RESIDENT	0	3
TENSE TOLERANCE	2	1
TONGUE FLICK & TOLERANCE	3	0
COMPLETE TOLERANCE	1	0
# REPETITIONS	6	6

Table 10a. Summary of reactions of orange resident females to the introduction of orange females with their orange covered by paint, and to males painted to imitate orange females.

	EXPERIMENTAL MANIPULATION	
	ORANGE ♀ X PLAIN MODEL	ORANGE ♀ X ORANGE MODEL
AVOIDANCE	2	0
INVESTIGATE & AVOIDANCE	4	1
INVESTIGATE & TOLERATE	0	5
# REPETITIONS	6	6

Table 10b. Summary of reactions of orange resident females to the introduction of models painted to imitate plain and orange lizards.

	DISPLAY	EXPERIMENTAL MANIPULATION			
		ORANGE ♀ x PAINTED ORANGE ♀	PAINTED ORANGE ♀	ORANGE ♀ x PAINTED ♂	
	PUSHUP	1	3	2	
EXPLORATORY	APPROACH	3	4	1	5
	GEN. TONGUE FLICK	2	1	1	2
	VENT TONGUE FLICK	3	1	1	2
AVOIDANCE & AGGRESSION	BACK ARCH	2	2	1	
	TURN SIDEWAYS	1			
	SIDESTEP	1			
	HOP AWAY			2	
	RUN AWAY	1		3	
	LEAP IN AIR			2	
	4-POINT POSITION	1	1	1	
	HISSING			1	
	GAPING	2	1		
COURTSHIP	NIPPING				1
	CHIN RUBBING				1
	TRY FOR NECK GRIP				4
	WALK AWAY	4	4	3	3

Table 11. Tabulation of behaviors observed between orange resident females, orange females covered with paint and males painted with orange (see Table 8).

lizard, but none of these resulted in further aggression or flight of either lizard. Painted orange females generally postured and displayed less than normal orange females in these encounters. Orange females responded to painted males in much the same way they responded to plain males (Table 8), with the exception of less general agitation and less posturing prior to flight or aggression. Males behaved as in previous experiments with exploratory and courtship behaviors.

Table 10b summarizes the reactions of resident orange females to introduced models painted with and without orange. Residents avoided plain models in all cases; four cases involved investigation prior to avoidance. Residents tolerated orange models in all cases but one where the model touched the female and startled her.

Table 12 shows that orange females respond to plain models much as they had to plain females and plain males (Table 9). We attempted to imitate the behavior of a male when manipulating the model but were unable to include typical male courtship behaviors such as slithering, nipping, and straddling, because previous experience had shown that lizards would not tolerate the touch of the models. Though models provided a visual simulation of G. wislizenii, it was not possible to duplicate the tactile properties of their bodies. Residents showed primarily exploratory behavior in response to orange models. In two cases the resident explored the model and then ran to another shrub and resumed hunting behavior, and in one case we accidentally touched the resident and she ran away and froze at the edge of a shrub and continued to observe the model.

	DISPLAY	EXPERIMENTAL MANIPULATION	
		ORANGE ♀ x PLAIN MODEL	ORANGE ♀ x ORANGE MODEL
	PUSHUP	2	1
EXPLORATORY	APPROACH		5
	GEN. TONGUE FLICK	4	5
	VENT TONGUE FLICK		3
AVOIDANCE	BACK ARCH	4	
	TURN SIDEWAYS	1	
	SIDESTEP	1	
	HOP AWAY	4	2
	RUN AWAY	4	3
	LEAP IN AIR	1	
	4- POINT POSITION	1	
	WALK AWAY	5	4

Table 12. Tabulation of behaviors observed between orange resident females, plain models, and orange models (see Table 8).

In summary, plain females avoid all plain lizards but are tolerant of orange females. Orange females display to all plain lizards and avoid plain models, while they tolerate other orange females and orange models. Orange females tolerate other orange females which have been painted to cover their orange. In three trials the resident was tolerant after tongue flicking the vent of the introduced female, in one trial the resident was completely tolerant, and in 2 trials the resident showed tense tolerance. Orange females avoided all painted males except one which did not attempt to court the resident female.

DISCUSSION

General Activity Patterns

Rose (1981) stated that, "It is doubtful that all lizards in a population are even simultaneously active in temperate regions even when climatic and/or thermal conditions are suitable for activity." Irwin (1965) found that least activity in Uta stansburiana was associated with the greatest intensity of solar radiation rather than the greatest temperature. This was true for G. wislizenii, which exhibited a bimodal activity pattern with lowest activity at mid day, and resumed activity in the afternoon when temperatures were still high, but the sun was not directly overhead.

Female movement and activity was less predictable than in males. One explanation for this difference is the sexual difference in cost versus the advantages of increased activity. Increased activity increases the likelihood of encountering prey items and/or mates, but also increases the risk of predation and imposes a metabolic price. Because G. wislizenii is a promiscuous breeder, males can increase their fitness by encountering (and successfully copulating with) as many females as possible. If high male activity is observed relative to female activity, it is possible that the "rewards" of increased contact with females is the selective force responsible for this difference.

Females must produce eggs, and are therefore subject to metabolic demands not experienced by males. If food resources and potential

mates are readily available without increased activity, it is to a female's advantage not to expend energy roaming. The more sedentary behavior of females as compared with males supports this idea. However, some females roamed widely. The reasons for differences in activity among females are not clear, but may include: 1) increased activity as a result of contact with males (e.g. avoidance), 2) searching for better hunting grounds, or 3) searching for appropriate egg-laying areas. Montanucci (1967) found that females were more active than males at the end of the breeding season, and that males hibernated earlier than females. He suggested that females may have to remain active to replenish fat stores necessary for hibernation which are depleted from egg-laying. My study was completed before the end of the breeding season, so I cannot document such a shift in activity for the Mickey Mountain population.

Inactivity may be as important as activity to survival and successful reproduction (Rose, 1981). Burrows therefore play an important role in the ecology of G. wislizenii. In all areas where we found G. wislizenii, the soil was suitable for the construction of burrows. McCoy (1967) suggested that mounded vegetation and the presence of rodent burrows were important characteristics of G. wislizenii habitat in Colorado. Rodent burrows were not used for estivation in our area, but we were unable to document the type of burrow used in hibernation.

Size and Growth Rate

The Alvord Basin lies within the northern extreme of G. wislizenii's distribution (Fig. 1), so it is not surprising that populations from this area vary in size and growth rate from their relatives further south. Parker and Pianka (1976) compared populations of G. wislizenii throughout their range (except in Oregon) and found that in northern populations individuals were smaller, and populations were denser than in southern populations. Parker and Pianka reported growth rates for adult females and males as .02 mm/day and .04 mm/day respectively. These rates are faster than those calculated for my population (.01 mm/day for both males and females). Adult size is ultimately greater in the southern portion of their distribution, therefore southern growth rates would be expected to exceed those of northern populations. Parker and Pianka reported growth rates in juvenile males and females as .19 mm/day and .24 mm/day respectively. I was only able to calculate growth rates for one juvenile male and one juvenile female (.37 mm/day and .52 mm/day). In both populations rapid growth in juveniles with respect to adults is observed. Rapid size increase observed in juveniles is adaptive both in predator deterrence and in reproduction. Parker and Pianka (1976) showed that egg weight/female body weight, (a measure of female reproductive effort), decreased with decreasing snout-vent length and age. This relationship suggests a reproductive advantage to rapid attainment of adult size.

Home Range Size

Home range size varies widely over G. wislizenii's distribution (Table 12). Two factors influencing the size of home range are the quality of available habitat and the length of time of data collection. Because these studies vary in the quality of habitat and the length of time of data collection, they are not directly comparable. I have included them to point out various biases and assumptions involved in determining the home range of a large, wide ranging lizard which does not engage in territorial behavior.

Abts (1976) suggested that lifetime home ranges of G. wislizenii in his study area were probably greater than those recorded during his study because his area was bordered by geographical and vegetational regions of inappropriate habitat. Snyder (1972) stated that limited habitat and a small sample size may have biased his home range sizes. Both Tollestrup (1972) and Tanner and Krogh (1974a) observed shifting of home ranges and nomadic behavior in G. wislizenii. Tollestrup included only one month of observations in her determination in an effort to avoid "gross overestimation" caused by the shifting of home ranges. Tanner and Krogh (1974a) calculated home ranges using data collected over a 3-year period.

In this study I have used all data points collected over a period of 2-1/2 months to determine home range size. Individual movement patterns suggested both nomadic behavior and shifting of home ranges, however, I was more interested in documenting the entire area used by

Moore (Oregon) May - July 1982	Max.	Min.	Average
♀	1.66	.001	.36
♂	1.92	.004	.62
Abts (Oregon) July 1974 - August 1975	Max.	Min.	Average
♀	.23	.01	.07
♂	.49	.04	.23
Snyder (California) June - July 1971	Max.	Min.	Average
♀	.32	.09	.20
♂	.46	.02	.17
Tollestrup (California) May - June 1976	Max.	Min.	Average
♀	1.2	.04	(only 2)
♂	2.8	.02	.14
Tanner & Krogh (Nevada) July 1966 - July 1969	Max.	Min.	Average
♀	1.54	.67	(only 2)
♂	2.35	----	----

Table 13. Comparisons of home range sizes over G.wislizenii's distribution. Home ranges are given in hectares. All of these studies used the minimum polygon method to determine home range.

an individual than in determining discrete areas of use which were subject to periodic shifts. Milstead (1972) suggested the term "home realm" for a total activity area, and "home range" for only the portion of "usual activity". He found that 22 points were necessary to make this distinction for the lesser earless lizard (Holbrookia maculata). I have selected the term home range to indicate the entire area used by an adult during the active season.

Though some nomadic behavior was observed in individuals of both sexes, male G. wislizeni wandered more than females. Increasing home range size for males is significantly correlated ($r = .744$; $p < .01$) with increasing numbers of data points, and suggests that males move about in a random way without showing preference for any one area.

Because males are more active than females, male data points are generally closer together both in time and in space than are female data points. This activity difference explains why male home ranges are generally smaller than female's when a small number of points are used to determine them, but larger when eight or more points are used (Table 5). As previously discussed (page 47), male and female activity are subject to different selective pressures. Abts (1976) found that male home ranges were large early in the season and decreased in size later into the summer, while female home ranges began small and increased toward the end of the season. Rose (1981) found that Sceloporus virgatus males were active 97% of the days during the breeding season, and females were active only 76% of the days; this pattern reverses during the non-breeding season. Because

my study was conducted during the first 2/3 of the breeding season, I may have biased my home range sizes by not including data from the end of the season. If females do become more active later in the season, my data would be skewed toward larger male ranges. This may be the case.

Generally, females were more sedentary than males, and though their data points were more widely separated in time, they were usually closer in space than those of males. It was common for a female to disappear for extended periods of time and reappear within 20 m of her last known location. Though more sedentary behavior was the rule for females, there were many exceptions, and the size of home ranges varied widely between individuals (Table 5).

Density

Tanner and Krogh (1974a) estimated density of G. wislizenii at the Nevada Test Site in southern Nevada as 5/ha.; a figure just over half the density calculated at Mickey Mountain. Turner et al. (1969) found densities <5/ha. at their study site in southern Nevada. Possible explanations for these density differences include habitat quality, sampling techniques, intraspecific aggression and predation. Sufficient information for comparing habitat quality is not available.

Sampling techniques are important because G. wislizenii generally follow a "gorge and rest" pattern of activity which makes it difficult to accurately determine how many individuals are present in

any area (Abts, 1976). Turner et al. (1969) worked with fenced populations, and did not have the problem of immigration and emigration, however, it is possible that the enclosures disrupted normal population dynamics. Tanner and Krogh (1974a) used data from an entire summer and did not take the question of immigration and emigration into consideration.

Intraspecific aggression outside of courtship attempts was rare in G. wislizenii at Mickey Mountain, and always occurred as low level aggressive postures and avoidance. Such behavior was typically exhibited by plain females in reaction to the presence of all other lizards (Table 8), and may have served as a spacing mechanism early in the season. Neither Tanner and Krogh nor Turner et al. observed any intraspecific aggression in G. wislizenii, but Tanner and Krogh hypothesized that the lack of social interactions observed in G. wislizenii, other than courtship, suggested the possibility of territoriality. The high degree of spatial and temporal overlap of home range at Mickey Mountain make territoriality in this population highly unlikely. Tollestrup (1972) provides an excellent discussion on the feasibility of home range defense in G. wislizenii.

Predation pressure may be greater in the southern portion of G. wislizenii's distribution than in the northern portion as indicated by a higher frequency of broken tails in the south (Parker & Pianka, 1976). We observed only one broken tail (partially regenerated) out of 115 lizards examined at Mickey Mountain. Providing that food is available to support dense populations, predation may be the prime

factor which determines G. wislizenii population density. This idea is untested at the present time.

Extensive overlap of female home ranges suggests that orange female coloration does not function as a spacing mechanism as originally hypothesized. Tolerant behavior exhibited between orange females (Table 7b) supports this conclusion.

Foraging Behavior

G. wislizenii is a generalist and an opportunistic feeder throughout its range (Stejneger, 1893; Pack, 1922; Van Denburgh, 1922; Stebbins, 1954; Tanner & Krogh, 1974a, b; McCoy, 1967; Montanucci, 1967; Pietruszka et al., 1981; Whitaker & Maser, 1981). Possible food items include blossoms, leaves, seeds, and lizards. Pietruszka et al. (1981) described predation on a Perognathus in Nevada which happened to be active during the day. Tollestrup (1972) described G. wislizenii predatory behavior as similar to that of the family Varanidae because of their habit of ambushing prey from concealed positions. She suggested that the nomadic tendencies of G. wislizenii might be adaptive in locating good ambush sites. Iguanids typically pursue only moving prey (Evans, 1961), but, Montanucci (1965) found that G. wislizenii silus could recognize Uta stansburiana even when they were motionless, and would dig them out of their burrows. He also noted that they sometimes swing their heads from side to side while stalking prey; a behavior which may aid in depth perception and distance judgement.

Montanucci (1967) found that G. wislizenii had a reflex attack to quick movements, and that lizards advancing nervously or dashing away were often chased, while bold movements or displaying lizards were often disregarded. It may be that the stylized posturing of C. tigris described earlier is an instinctive or reflex reaction to unexpected encounters with G. wislizenii and does not reflect any present predatory relationship between the species.

G. wislizenii at Mickey Mountain preyed only on invertebrates. Flying insects, and particularly cicadas, were the primary food items. Because G. wislizenii is an opportunistic feeder, this selection most likely reflects the abundance of these items, rather than a rigid preference for them. Results from Whitaker and Maser's study (1981) which show that G. wislizenii preyed exclusively on insects and spiders support the idea that members of northern populations rarely if ever prey on vertebrates.

Scansorial behavior was common in G. wislizenii at Mickey Mountain. This behavior may provide thermal relief from the substrate as well as aid in foraging for shrub dwelling insects. On many occasions we observed both G. wislizenii and C. tigris to hunt within or on the top of a shrub. On one occasion, a G. wislizenii courtship was carried on entirely within the branches of a big sage. The courtship continued for 9 minutes and included most of the typical courtship behaviors (Figure 8).

Although G. wislizenii appears to be primarily a visual hunter, the role of olfaction and audition should not be overlooked. Iguanids have historically been considered to be highly visual

animals, but recent studies have shown the genera Sceloporus and Phrynosoma to respond with species specific behavior to olfactory cues from conspecifics (Duvall, 1979 and 1981; Tollestrup, 1981; Simon et al., 1981). There have been no studies which have addressed the question of the possible role of olfaction in iguanid foraging. It is unlikely that olfaction is of any assistance in locating aerial prey (as were the selected items in our area), but it may be important in locating vertebrate prey in the southern regions of G. wislizenii's distribution.

The role of audition in foraging behavior of G. wislizenii is poorly understood. Jorgensen et al. (1963) first documented the vocalizations of G. wislizenii and described them as similar to those made by Coleonyx variegatus from the same area. Wever et al. (1966) found that although their ear is undifferentiated as in all iguanids, G. wislizenii was highly sensitive to a range of 300-700 cycles per second (cps). This is also the range that most geckos are most sensitive to. G. wislizenii was actually more sensitive than geckos to this range. Summation due to all of the hair cells responding to this limited range is probably responsible for the sensitivity (Wever et al., 1966). We observed G. wislizenii to respond to auditory cues from aerial prey, but did not witness any vocalizations.

Social Behavior

Only a few studies have described social behavior in G. wislizenii, and all have emphasized the lack of it as compared with

other iguanids. Tollestrup (1972) described the displays of G. wislizenii as including pushups, simple head bobs, and posturing, but pointed out the simplistic nature of their social behavior as compared with their closest relative, Gambelia silus (an endemic species of leopard lizard from the San Joaquin Valley of California). Montanucci (1970) and Snyder (1972) noted head bobbing behavior by male G. wislizenii, and interpreted these displays as aggressive behaviors indicating intrasexual intolerance and/or territoriality. Enclosure experiments by Carpenter (1967) showed no intraspecific display or aggression in G. wislizenii of either sex. Montanucci (1967) described kicking and clawing by female G. wislizenii in response to courtship attempts by males, but also indicated that females may solicit male attention prior to copulation by approaching males and licking them.

The behavioral repertoire of G. wislizenii as documented in this study is typical of the family Iguanidae. Several factors may contribute to the lack of social behavior observed in southern populations. First of all, there have been no studies which specifically addressed the subject of social behavior. Second, it is possible that northern populations are more social as a result of higher population densities, and therefore exhibit more variety in their behavior than do southern populations. Third, it is possible that less observations on social behavior have been made in southern populations because in sparse populations social interactions occur less frequently. The lack of detailed information on G. wislizenii

behavior in other areas of their range prohibits comparative discussion of regional behavioral differences.

Male-Male Interactions

In all cases observed, males encountering other males courted them as they courted plain females. Often the two males courted each other alternately, but no aggression of any kind was observed. Toward the end of the breeding season these male-male courtships were observed more frequently. It is possible that as males encounter less receptive females, they are likely to court any lizard which does not display overt aggression toward them. This behavior persists in spite of sexual cues that should be available such as olfaction (vent-tongue flicking) and behavioral response of the recipient, which indicate that the recipient is not of the appropriate sex. Noble and Teale (1930) suggested that the incidence of males mating with males, and even shedding sperm in their cloaca, is very high in lizards. Therefore, any mechanism which reduces such useless matings should be selected for.

Some lizards use color, olfaction, or morphological differences such as dewlap size in sex determination (Evans, 1936 and 1938b; Greenberg, 1945; Fitch, 1954 and 1958; Carpenter, 1962b; Ferguson, 1966). In others, sex recognition is dependent on the response of the courted individual (Noble, 1933; Carpenter, 1961b and 1962a; Hardy, 1962). G. wislizeni males appear to belong to the second

group, however, females do use olfaction in sex determination (Table 10a).

What appears to be poor sex discrimination in males may actually be adaptive if some females become sexually active later in the season than the majority of the females. Some females at Mickey Mountain developed their orange coloration as late as the second week of July (most females had theirs by mid to late June). Those turning in July may have been juvenile females coming into reproduction condition for the first time. Males who continue to court plain lizards may encounter these young females. It is also possible that inexperienced females do not respond to males the way that experienced females do, and therefore the passive behavior of male recipients may not provide a useful cue in sex determination. No courtships were observed with juvenile females.

Courtship Behavior

In most male iguanids, male courtship behavior develops whether females are present or not (Noble & Teale, 1930), and males will copulate with most receptive females. Females may be highly selective, showing positive discrimination for dominant males (Evans, 1938b) and rejecting males once they are gravid (Fitch, 1940; Greenberg, 1945). In many species the female will solicit male courtship by head nodding (Evans, 1938a; Greenberg & Noble, 1944) caudal display (Evans, 1953) or approach and tactile stimulation (Fitch, 1956; Blair, 1960; Carpenter, 1961a, b; Harris, 1964;

Tollestrup, 1981). Many researchers have reported a high number of courtships relative to copulations in iguanids (Greenberg, 1943; Irwin, 1965; Yedlin & Ferguson, 1973). Male courtship may be an important primer for female receptivity by providing tactile stimulation (Carpenter & Ferguson, 1977).

Male G. wislizenii court all conspecifics which do not display overt aggression toward them. Females were more discriminating, and avoided all plain lizards, thus avoiding all potential males. This behavior forced males to pursue them in order to initiate courtship. Males which were able to court successfully were those exhibiting patience, speed and agility in their attempts to gain a neck grip on the female. These qualities are desirable in G. wislizenii not only for courtship, but in foraging behavior and predator avoidance as well (see previous discussion). Females may be exercising mate choice by behaving in this way, which exerts selective pressure on males to display characteristics which will improve their offspring's chances of survival.

Female G. wislizenii develop orange coloration at, or about the time of ovulation (Tanner & Krough, 1974a), therefore it is likely that they copulate just before the onset of coloration, or as it begins to appear. Some iguanid females can store sperm; Uta stansburiana can store sperm for 81 days, and Anolis caroliensis can store sperm for up to six months (Porter, 1972). The sperm storage capability of G. wislizenii is unknown. Most successful courtships observed involved plain females, however, we did observe males with neck grips on orange females twice. Once a male secures a grip, he

will straddle the female and ride her for up to three hours before actually copulating. During this period, the female is conspicuous to predators and unable to feed. Therefore, females should discourage male courtship once they are gravid to prevent such unnecessary incapacitation.

Orange females do avoid males as predicted (Tables 7b and 10a), but display overt aggression which sharply contrasts with the coy behavior of plain females. The high level aggressive postures and hissing of orange females acts as an effective deterrent to male courtship. Most males do not attempt to court aggressive orange females, but some males adopt a rape strategy (see previous discussion). The rape strategy is interesting because it is so different from the stylized courtship, and because it was never observed to end in a successful copulation, or even a secure neck grip. In order to determine if this behavior is adaptive, it would be necessary to know: 1) is sperm competition occurring? 2) can one clutch be sired by more than one male? 3) what is the insemination success for rape versus courtship? As mentioned above, we did observe males with neck grips on orange females, but we did not observe the events leading up to this situation. Therefore, we cannot determine if rape or courtship was used in securing the neck grip. Some females were observed to accept courtships just as they were developing their coloration. I can only note this behavior as an interesting phenomenon, because the information needed for further discussion is not currently available.

Female-Female Interactions

Female-female interactions involving free-ranging lizards were rare. The reactions of resident females to introduced females depended both on the color and on the behavior of the introduced lizard. Plain females were intolerant of each other, while they tolerated orange females. Orange females were tolerant of each other, especially if they tongue flicked one another's vents. This tongue flicking suggests that females are receptive to olfactory and/or gustatory cues in sex determination. The information received may tell them that the animal being investigated is: 1) a female, 2) not a male. It is not clear at this time which type of information they receive. Plain females do tongue flick courting males, but orange females do not let males get close enough to them for tongue flicking, as this would permit them to try for a neck grip. In general terms, plain females react to other plain females as though they were males, and orange females show indifference or friendly tolerance (allowing body contact) toward other orange females.

Miscellaneous Behaviors

The action of G. wislizenii rubbing their cloacas on the substrate may be a mechanism for distributing pheromones (see previous discussion). It is possible that the waxy exudates of the femoral pores may be a medium for pheromones, as may be secretions from the cloaca. Such olfactory and/or gustatory cues could serve to

communicate the presence of a conspecific, and possibly the sex of that individual. Because G. wislizenii was not observed to engage in any intraspecific aggression (outside of courtship attempts by males), it is unlikely that these cues have a role in territoriality. It is possible that individuals will not choose an area for hunting in which they have encountered the scents of many individuals; however, behavioral observations indicate that G. wislizenii individuals do not maintain exclusive areas of activity.

The possibility of males exhibiting "female tending" is very intriguing because they show no other territorial tendencies (see previous discussion). Female tending has been described both in teids (Carpenter, 1962a; Hirth, 1963; Kennedy, 1968) and in iguanids (Tollestrup, 1981). In order to determine if it were to a male's advantage to prevent other males from access to a female he had previously copulated with, it would be necessary to know: 1) if sperm competition occurs, and if so, over what period of time is this possible, 2) can one clutch of eggs be sired by more than one male, 3) how important is the time which he spends tending one female which he could be spending encountering and mating with other females. Because this behavior was only observed once, it may be that the male happened to be nearby, and the sight of a courtship triggered his own courtship behavior to resume.

The Role of Orange Coloration in Social Behavior

Color is an important behavioral stimulus in iguanid lizards, functioning in sex determination and territoriality (Noble & Teale, 1930; Evans, 1936; Greenberg, 1945; Vinegar, 1972). Display of certain colors may prevent intraspecific aggression or inappropriate courtships by advertising both the sex and the breeding condition of individuals (Fitch, 1956; Clarke, 1965; Carpenter, 1967; Vinegar, 1972; Medica et al., 1973).

Female Crotaphytus collaris develop an orange coloration similar to that of G. wislizenii which Carpenter (1967) suggested might be a signal to males that a female was unreceptive. Fitch (1967) found that the "red-orange markings" of female C. collaris inhibited male courtship. Similar markings appear for two to three weeks on juvenile males just before they reach sexual maturity; the reaction of males to juveniles at this time is unknown (Fitch, 1967). Fitch (1956) found that experienced male C. collaris were inhibited by the display of orange female coloration, while young males pursued females until the females became overtly aggressive. This suggests that male response to orange coloration may be a learned behavior. Clarke (1965) found that female Holbrookia propinqua, Cophosaurus texanus, and Callisaurus draconoides all develop special breeding colorations which he believed discourage male courtship.

Many authors have speculated about the function of orange breeding coloration in G. wislizenii as discussed in the introduction. Medica et al. (1973) induced orange spotting in non-

ovariectomized females in 7-21 days by treating them with FSH (follicle-stimulating hormone). His ovariectomized females developed orange when progesterone was administered; estrogen had a priming effect on progesterone causing a more rapid appearance of color, but was ineffective when administered alone. Cooper and Ferguson (1972a, b, 1973) showed estrogen to have a priming effect on progesterone, hastening the onset of orange spotting in female C. collaris. Licht (1970) found that mammalian FSH was a more potent stimulator of gonadal growth than mammalian LH in female lizards, and that FSH induced normal ovulation while LH did not. Licht (1979) suggested that lizards may lack LH, and therefore FSH may replace the functions of LH in lizards. Licht cautions that only exogenous hormones have been used in studies so far, and the effects of endogenous hormones may differ. FSH has been shown to increase receptive behavior in female Uta stansburiana (Ferguson, 1966). It appears that orange coloration in female G. wislizenii is initiated by high levels of progesterone following ovulation. The effect of changing hormone levels on social behavior is unknown.

General Discussion

Many studies have addressed the importance of intensity and distribution of colors and patterns in the social behavior of animals. Color has been shown to be important in the attraction of mates (Semler, 1971; Haas, 1976), in aggressive intraspecific displays (Noble & Teale, 1930; Noble, 1936; Fitch, 1940; Greenberg,

1945; Ferguson, 1966; Vinegar, 1972; Stacey & Chiszar, 1977), and on signaling social dominance (Marler, 1955; McAllister, 1958; Barlow, 1973; Rohwer, 1977; Ketterson, 1979).

Darwin (1871) suggested that sexual selection could account for secondary sexual characteristics which had no direct survival value for the individual. Semler (1971) found that female three-spined sticklebacks (Gasterosteus aculeatus) chose red males over plain males, but that red males are preyed on more often than plain males because they are more conspicuous. Haas (1976) found that brightly colored male Notobranchius guentheri copulate more often than plain males because they are more visible to females in the turbid waters of ephemeral ponds they inhabit. Due to the temporary nature of their environment, females copulate with the first male they encounter, and reproduction proceed rapidly. Brightly colored male N. guentheri also suffer high mortality from avian predators as to plain males. Selander (1965) suggested that selection for sexual dimorphism in monogamous birds may be balanced by increased male mortality (resulting from elaborate secondary sex characteristics), which would decrease competition for females. The orange coloration of female G. wislizenii does make them more conspicuous than males, however, their sedentary nature and "sit and wait" method of foraging, decrease the likelihood of their detection by visual predators. As previously discussed, gravid females are quite vulnerable to predation when males are "riding" them with a neck grip, and prevention of this unnecessary incapacitation should be strongly selected for.

The use of colors and patterns in intraspecific aggression has been well-documented in fish (Stacey & Chiszar, 1977), lizards (Noble & Teale, 1930; Fitch, 1940; Vinegar, 1972), and birds (Noble, 1936). Noble (1936) described the use of brilliant yellow tail feathers in the common flicker to intimidate members of the same sex and therefore gain an advantage in competition for mates. Noble warned that sexual selection may be an illusion in some species, and that elaborate colors may arise primarily to intimidate rather than to attract conspecifics. It appears that orange coloration in female G. wislizenii aids in deterring undesirable courtships, but the question of male attraction to this color remains unanswered at this time.

Color intensity and pattern has been shown to be an important indicator of social dominance in chaffinches (Marler, 1955), Harris sparrows (Rohwer, 1977), dark-eyed juncos (Ketterson, 1979) and midas cichlids (Barlow, 1973). McAllister (1958) showed that dominant Gambusia hurtadoi were brilliant yellow while subordinates were more drab. If the dominant G. hurtadoi was removed, another individual would acquire the brilliant coloration. At low population densities, dominance was less complete and subordinates were brighter in coloration. It is unlikely that orange coloration serves as a signal of social dominance in G. wislizenii because: 1) color intensity varies with reproductive condition but not between individuals in the same reproductive condition; 2) observations of social behavior reveal no indication of aggression or dominance within the sexes.

Conclusions

Results from this study indicate that orange coloration in breeding female G. wislizenii serves as a deterrent to male courtship, and as an appeasement signal to other females. It is to a gravid female's advantage to avoid further contact with males which would make them more conspicuous to predators and interfere with their foraging behavior. It is also to a female's advantage to recognize other females and not waste energy displaying high level aggressive postures and avoidance toward females as they must toward males to discourage courtship. Males respond both to color and aggressive postures of orange females. It is possible that learning is involved in the recognition of orange females as unreceptive by color alone as was seen in C. collaris (Fitch, 1956).

It is my conclusion that orange female coloration serves to prevent unnecessary expenditures of energy on the part of both males and females, as well as preventing gravid females from excessive exposure to predation and interrupting their feeding.

LITERATURE CITED

- Abts, M.L. 1976. Thermal ecology and movement in the leopard lizard Gambelia wislizenii. M.A. Thesis, Portland State Univ. 133 pp.
- Banta, B.H. 1962. Preliminary remarks upon the zoogeography of the lizards inhabiting the great basin of the western U.S. Wasman J. Biol. 20(2): 253-287.
- Barlow, G.W. 1973. Competition between color morphs of the polychromatic Midas Cichlid Cichlasoma citrinellum. Sci. 179 (4075): 806-807.
- Blair, W.F. 1960. The rusty lizard. A population study. Univ. Texas Press, Austin 185 pp.
- Brattstrom, B.H. 1974. The evolution of reptilian social behavior. Amer. Zool. 14: 35-49.
- Brooking, W.J. 1934. Reptiles and amphibians of Malheur Co. Copeia 1934: 93-95.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammalogy 24: 346-352.
- Calhoun, J.B. and J.N. Casby. 1958. Calculations of home range and density of small mammals. U.S. Public Health Monograph 55: 1-24.
- Carpenter, C.C. 1961a. Patterns of social behavior of Merriam's canyon lizard (Sceloporus m. merriami-Iguanidae). S.W. Nat. 6(3-4): 138-148.
- _____. 1961b. Patterns of social behavior in the desert iguana Dipsosaurus dorsalis. Copeia 1961 (4): 396-405.
- _____. 1962a. Patterns of behavior in two Oklahoma lizards. Am. Midl. Nat. 67: 132-151.
- _____. 1962b. A comparison of the patterns of display of Urosaurus, Uta, and Streptosaurus. Herpetologica 18(3): 145-152.
- _____. 1967. Aggression and social structure in Iguanid lizards in: Lizard Ecology: A Symposium (W.W. Milstead; ed.) pp. 87-105. Univ. Missouri Press, Columbia.
- Carpenter, C. & G.W. Ferguson. 1977. Variation and Evolution of Stereotyped Behavior in Reptiles. pp. 335-554 In: Biology of the Reptilia, C. Gans editor, Academic Press, N.Y.
- Clark, W.H. 1974. Arboreal behavior of the leopard lizard Crotaphytus wislizenii in western Nevada. Trans. Kansas Acad. Sci. 77(1): 68.

- Clarke, R.F. 1965. An ethological study of the iguanid lizard genera Callisaurus, Cophosaurus and Hokbrookia. Emporia State Research Studies 13: 1-66.
- Cooper, W.E. Jr., & G.W. Ferguson. 1972a. Steroids and color change during gravidity in the lizard Crotaphytus collaris. Gen. Comp. Endocrinol. 18: 69-72.
- _____. 1972b. Relative effectiveness of progesterone and testosterone as indicators of orange spotting in female collared lizards. Herpetologica 28: 64-65.
- _____. 1973. Estrogenic priming of color change induced by progesterone in the collared lizard Crotaphytus collaris. Herpetologica 29: 107-110.
- Darwin, C. 1871. The descent of man to selection in relation to sex. 2 vols. London: Murray.
- Daubenmire, R.F. 1959. Canopy coverage method of vegetation analysis. N.W. Sci. 33: 43-64.
- Duvall, D. 1979. Western fence lizard (Sceloporus occidentalis) chemical signals I. Conspecific discriminations and release of a species-typical visual display. J. Exp. Zool. 210(2): 321-325.
- _____. 1981. Western fence lizard (Sceloporus occidentalis) chemical signals. II. A replication with naturally breeding adults and a test of the Cowles and Phelan hypothesis of rattlesnake olfaction. J. Exp. Zool. 218: 351-361.
- Evans, L.T. 1936. A study of social hierarchy in the lizard Anolis carolinensis. J. Genetic Psych. 48: 88-110.
- _____. 1938a. Cuban field study on territoriality of the lizard Anolis sagrei. J. Comp. Psych. 25: 97-125.
- _____. 1938b. Courtship behavior and sexual selection of Anolis. J. Comp. Psychol. 26: 475-497.
- _____. 1953. Tail display in an iguanid lizard Liocephalus carinatus coryi. Copeia 1953: 50-54.
- _____. 1961. Structure as related to behavior in the organization of populations in reptiles, pp. 148-178. in: Vertebrate Speciation (W. W. Blair; ed.) Univ. Texas Press, Austin.
- Ferguson, G.W. 1966. Releasers of courtship and territorial behavior in the side-blotched lizard Uta stansburiana. Anim. Behav. 14: 89-92.

- Fitch, H.S. 1940. Field study of the growth and behavior of the fence lizard. *Univ. Cal. Publ. Zool.* 44: 151-172.
- _____. 1954. Life history and ecology of five-lined skink, Eumeces fasciatus. *Univ. Kansas Publ. Mus. Nat. History* 8(1): 1-156.
- _____. 1956. An ecological study of the collared lizard (Crotaphytus collaris). *Univ. Kansas Publ. Mus. Nat. History* 8(3): 215-274.
- _____. 1958. Natural history of the six-lined race-runner Cnemidophorus sexlineatus. *Univ. Kansas Publ. Mus. Nat. History* 11: 11-62.
- _____. 1967. Discussion, p. 75 in: Lizard Ecology: A Symposium (W.W. Milstead, ed.) Univ. Missouri Press, Columbia.
- Greenberg, B. 1943. Social behavior of the western banded gecko Coelonyx variegatus. *Physiol. Zool.* 16: 110-122.
- Greenberg, B. 1945. Notes on the social behavior of the collared lizard. *Copeia* 1945: 225-230.
- Greenberg, B. & G.K. Noble. 1944. Social behavior of the American chameleon (Anolis carolinensis Voigt). *Physiol. Zool.* 17(4): 392-439.
- Haas, R. 1976. Sexual selection in Notobranchius guentheri (Pisces: Cyprinodontidae). *Evolution* 30: 614-622.
- Hardy, D.F. 1962. Ecology and behavior of the six-lined racerunner, Cnemidophorus sexlineatus. *Univ. Kansas Sci. Bull.* 43:3-73.
- Harris, V. 1964. The Life of the Rainbow Lizard. Hutchinson & Co., Ltd., London. 174 p.
- Hayne, Don W. 1949. Calculation of size of home range. *Jour. Mammal.* 30(1): 1-18.
- Hirth, F.H. 1963. The ecology of two lizards on a tropical beach. *Ecol. Monogr.* 33: 83-112.
- Holmgren, N. 1972. Plant Geography of the Intermountain Region. In: Cronquist, A. et al. Intermountain Flora I, Hafner, N.Y. pp. 114-126.
- Irwin, L.N. 1965. Diel activity and social interaction of the lizard Uta stansburiana stejnegeri. *Copeia* 1965: 99-101.
- Jennrich, R.I. and F.B. Turner. 1969. Measurement of non-circular home ranges. *J. Theoret. Biol.* 22: 227-237.

- Johnsgard, J.S. 1963. Temperature and the water balance for Oregon weather stations. Spec. Rept. 1560, Agric. Exp. Stn., Oregon State University, Corvallis, Oregon 127pp.
- Jorgensen, C.D., A.M. Orton, W.W. Tanner. 1963. Voice of the leopard lizard Crotaphytus wislizenii Baird & Girard. Utah Acad. Proc. 40: 115-116.
- Jorgensen, C.D. & W.W. Tanner. 1963. Application of density probability function to determine home ranges of Uta stansburiana stansburiana and Cnemidophorus tigris tigris. Herpetologica 19(2): 105-115.
- Kennedy, J.P. 1968. Observations on the ecology and behavior of Cnemidophorus guttatus and Cnemidophorus deppei (Sauria: Teiidae) in S. Veracruz. J. Herpetol. 2: 87-96.
- Ketterson, E.D. 1979. Status signaling in dark-eyed juncos. Auk 96: 94-99.
- Licht, P. 1970. Effects of mammalian gonadotropins (Ovine FSH and LH) in female lizards. Gen. Comp. Endocrinol. 14: 98-106.
- Licht, P. 1979. Reproductive endocrinology of reptiles and amphibians: gonadotropins. Ann. Rev. Physiol. 41: 337-351.
- Marler, P. 1955. Studies of fighting Chaffinches. (2) The effect on dominance relations of disguising females as males. Anim. Behav. 3: 137-146.
- McAlister, W.H., 1958. The correlation of coloration with social rank in Gambusia hurtadol. Ecology 39 (3): 477-482.
- McCoy, C.J. 1967. Natural history notes on Crotaphytus wislizenii (Reptilia:Iguanidae) in Colorado. Am. Midl. Nat. 77(1): 138-146.
- McKee, B. 1976. Cascadia, The Geologic Evolution of the Pacific Northwest. McGraw-Hill, N.Y. 394 pp.
- Medica, P.A.; F.B. Turner; D.D. Smith. 1973. Hormonal induction of color change in female leopard lizards, Crotaphytus wislizenii. Copeia 1973 (4): 658-661.
- Milstead, W.W. 1972. More on lizard home ranges. Herp. Rev. 4: 83-84.
- Montanucci, R.R. 1965. Observations on the San Joaquin leopard lizard Crotaphytus wislizenii silus Stejneger. Herpetologica 21(4): 270-283.
- _____. 1967. Further studies on leopard lizards Crotaphytus wislizenii. Herpetologica 23(2): 119-126.

- _____. 1970. Analysis of hybridization between Crotaphytus wislizenii and Crotaphytus silus (Sauria: Iguanidae) in California. Copeia 1970(1): 104-123.
- Moseley, K.T. Jr. 1963. Behavior patterns of the collared lizard (Crotaphytus collaris collaris). M.S. Thesis, Univ. Oklahoma, Norman. 40 pp.
- Mueller-Dombois, D. & H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley N.Y. pp. 111-113.
- Noble, G.K. 1933. The mating behavior of lizards; it's bearing on the theory of sexual selection. Ann. New York Acad. Sci. 35: 25-100.
- _____. 1934. Experimenting with the courtship of lizards. Nat. History 34(1): 3-15.
- Noble, G. 1936. Courtship and sexual selection of the flicker (Colaptes auratus luteus) Auk 52: 269-282.
- Noble, G.K. & H.K. Teale. 1930. The courtship of some iguanid and teiid lizards. Copeia 1930: 54-56.
- Nussbaum, R.A., E.D. Brodie, Jr., & R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. Univ. Press of Idaho 332 pp.
- Pack, H.J. 1922. Food habits of Crotaphytus wislizenii Baird and Girard. Proc. Biol. Soc. Washington 35: 1-4.
- Parker, W.S. & E.R. Pianka. 1976. Ecological observations on the leopard lizard Crotaphytus wislizenii in different parts of it's range. Herpetologica 32(1): 95-114.
- Pietruszka, R.D.; J.A. Wiens; & C.J. Pietruszka. 1981. Leopard lizard predation on Perognathus. J. Herpetol. 15(2): 249-250.
- Porter, K.R. 1972. Herpetology. W.B. Saunders Co. Philadelphia.
- Rose, B. 1981. Factors affecting activity in Sceloporus virgatus. Ecology 62: 706-716.
- Rohwer, S. 1977. Status signaling in Harris sparrows: Some experiments in deception. Behavior 61(1-2): 107-129.
- Selander, R.K. 1965. On mating systems and sexual selection. Amer. Nat. 99: 129-140.
- Semler, D.E. 1971. Some aspects of adaptation in a polymorphism for breeding colors in the three-spined stickle-back (Gasterosteus aculeatus). J. Zool (Land) 165: 291-302.

- Simon, C.A.; K. Gravelle; BeBissinger, I. Eiss; R. Rubae. 1981. The role of chemoreception in the iguanid lizard Sceloporus jarrovi. Anim. Behav. 29: 46-54.
- Snyder, J.D. 1972. An ecological investigation of sympatric populations of the lizards Crotaphytus collaris and Crotaphytus wislizenii. M.A. Thesis, San Francisco State University, 88 pp.
- Stacey, P.B. & D. Chiszar. 1977. Body color and pattern and the aggressive behavior of male pumpkinseed sunfish (Lepomis gibbosus) during the reproductive season. Behav. 64: 271-297.
- Stebbins, R.C. 1954. Amphibians and Reptiles of Western North America. McGraw-Hill Book Co., New York.
- _____. 1966. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Co., Boston.
- Stejneger, L. 1893. Annotated list of reptiles and batrachians collected by the Death Valley expedition in 1891 - with descriptions of new species. North Amer. Fauna 7: 159-228.
- Tanner, W.W. and J.E. Krogh. 1974a. Ecology of leopard lizard Crotaphytus wislizenii at Nevada test site, Nye Co., Nevada. Herpetologica 30(1): 63-72.
- _____. 1974b. Variations in activity as seen in four sympatric lizard species of southern Nevada. Herpetologica 30(3): 303-308.
- Taylor, W.P. 1912. Field notes on amphibians, reptiles, and birds of northern Humboldt Co., Nevada. Univ. Cal. Publ. Zool. 7(10): 319-436.
- Tinkle, D.W. 1959. Observations on the lizards Cnemidophorus tigris, Cnemidophorus tessellatus and Crotaphytus wislizenii. S.W. Nat. 4(4): 195-200.
- _____. 1967. Home range density, dynamics, and structure of a Texas population of the lizard Uta stansburiana. in: Lizard Ecology: A Symposium (W.W. Milstead ed.) Univ. Missouri Press, Columbia.
- Tinkle, D.W.; D. McGregor & S. Dana. 1962. Home range ecology of Uta stansburiana stejnegeri. Ecology 43(2): 223-229.
- Tollestrup, K. 1972. Ecology, social structure, and foraging behavior of two closely related species of leopard lizards Gambelia silus and Gambelia wislizenii. Ph.D. dissertation, U.C. Berkeley, 146 pp.

- _____. 1981. The social behavior and displays of two species of horned lizards, Phrynosoma platyrhinos, and Phrynosoma coronatum. Herpetologica 37(3): 130-141.
- Turner, F.B. 1971. Estimating lizard home ranges. Herpetol. Rev. 3(4): 77.
- Turner, F.B.; J.R. Lannom Jr.; P.A. Medica; & G.A. Hoddenbach. 1969. Density and composition of fenced populations of leopard lizards (Crotaphytus wislizenii) in southern Nevada. Herpetologica 25(4): 247-257.
- Van Denburgh, J. 1922. Reptiles of western North America vol. I, lizards. Occ. Pap. Cal. Acad. Sci., 10: 1-611.
- Vinegar, M.B. 1972. The function of breeding coloration in the lizard Sceloporus virgatus. Copeia 1972: 660-664.
- Walker, G.M. 1969. Geology of the Great Basin and Range Province. Oregon Dept. Geol. and Min. Ind. Bull. No. 64, pp. 83-88.
- Wever, E.G.; M.C. Hepp-Reymond; & J.A. Vernon. 1966. Vocalization and hearing in the leopard lizard. Proc. Nat. Acad. Sci. 55: 98-106.
- Whitaker, J.O. & C. Maser. 1981. Food habits of seven species of lizards from Malheur Co., southwestern Oregon. N.W. Sci. 55(3): 202-208.
- Woodbury, A.M. 1959. Clasp ing behavior of the leopard lizard. Herpetologica 15: 118.
- Yedlin, I.N.; & G.W. Ferguson. 1973. Variations in aggressiveness of free-living male and female collared lizards. Crotaphytus collaris. Herpetologica 29(3): 268-275.

APPENDICES

APPENDIX 1

DEFINITIONS OF BEHAVIORS

1. General Agitation

Pushup - repeated flexion and extension of the front legs; normally performed with head raised.

2. Exploratory

Approach - movement of one individual toward another

General Tongue Flick - extension and retraction of the tongue; may be directed in the air, or around protruding objects, e.g., rocks, sticks.

Vent Tongue Flick - tongue flick directed at the cloaca of a conspecific.

3. Avoidance and Aggression

Back Arch - raising of back generally accompanied by extension of the legs.

Turn Sideways - movement which alters the orientation of two conspecifics such that they become perpendicular to one another.

Sidestep - lateral movement of one individual relative to another which generally increases the distance between them while maintaining the original orientation.

Walk Away - voluntary movement of one individual away from another in an unagitated manner.

Stiff Walk - An exaggerated gait performed with stiff joints.

Hop Away - hopping motion which alters the orientation of two conspecifics and/or increases the distance between them.

Leap in Air - Vertical motion of an individual which may or may not alter its orientation or distance from a conspecific.

Run Way - rapid retreat of one conspecific from another.

Bipedal Run - running performed on the hind legs only, with the body tilted upward, and held off the substrate.

4-Point Position - all four legs are extended, the back arched, and the tail is held above the substrate; the head is often held below the level of the shoulder.

Gaping - opening the mouth and exposing the black area at the back of the throat; generally oriented toward an aggressor.

Hissing - controlled release of air from the throat region which produces a unique sound; performed in highly aggressive encounters.

4. Courtship

Slither - undulating movements of one individual over another; generally performed by a male, back and forth across a female.

Straddle - a superior position of one individual relative to another in which the superior individual's legs are placed on either side of the lower animal.

Try For Neck Grip - attempt on the part of a male to secure a hold on the loose skin of a conspecific's neck; generally performed on females, this hold is prerequisite to successful copulation.

Leg Grip - one individual grasps the leg of another in it's jaws; generally performed by a male on a female.

Chin Rubbing - one individual rubs its chin on another; generally performed by a male on a female

Nipping - superficial grasping and releasing of a conspecific; generally performed by a male on a female.

Flipping Over - male grasps female by the leg and flips her on her back by a rapid and violent contortion of his body; generally used in the absence of normal courtship.

5. Other

Tail Arch - tail is arched and held above the substrate; performed while defecating, as well as without defecation, also a component of aggressive female postures (see 4-point position).