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by

Barbara Ellis Bissinger

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of the requirements for the degree of

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in

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of the City University of New York

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Abstract

HOMING BEHAVIOR, SUN-COMPASS ORIENTATION, AND THERMOREGULATION IN THE LIZARD (SCELOPORUS JARROVI): THE ROLE OF THE PARIETAL EYE

by

Barbara Ellis Bissinger

Advisor: Professor Carol A. Simon

Normal lizards (*Sceloporus jarrovi*) were displaced in the field distances ranging from 50 to 200 m. Adult lizards returned home from all displacement distances, while juvenile homing success was poor at distances greater than 50 m. One-year old adult lizards had significantly lower homing success than older lizards.

The role of the parietal eye in *S. jarrovi* homing was investigated by displacing three groups of lizards approximately 150 m: 1) normal lizards, 2) sham-treated lizards (paint placed alongside parietal eye), and 3) experimental lizards (parietal eye covered with a layer of paint). Significantly fewer experimental lizards returned home (20%) than either normal (61%) or sham-treated lizards (57%). In control studies the parietal eye treatment did not affect daily activity patterns, home range size, or survivorship.

Radio-tracking of displaced *S. jarrovi* showed that normal and sham-treated lizards were significantly oriented towards home one-half hour after displacement and moved in pathways to home that were significantly non-random. Experimental lizards, however, were not significantly oriented towards home, either one-half or three and one-half hours later, and moved randomly where they were released. The mean body temperatures of these radio-tracked lizards showed no significant differences among the three treatment groups.

Sun-compass orientation in S. jarrovi was investigated by displacing four groups of transmitter-equipped lizards: 1) normal lizards on a natural light-dark (LD) cycle, 2) normal lizards entrained to a six-hour advanced LD cycle, 3) experimental lizards on a natural LD cycle, and 4) experimental lizards on the advanced LD cycle. Normal lizards on the natural LD cycle showed significant orientation towards home 30 minutes after release. The normal lizards on the six-hour phase advance, however, shifted their initial orientation approximately 90° counterclockwise from home. These results demonstrate that S. jarrovi can use a time-compensated, sun-compass mechanism to orient towards home. Both groups of experimental lizards moved in random directions after displacement. This result suggests that the parietal eye, and not the lateral eyes, is perceiving the celestial cues utilized in this sun-compass orientation.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

I. INTRODUCTION

The long-distance orientation behaviors of animals, including both migration and homing, have fascinated biologists for decades. Early studies of the mechanisms underlying these remarkable behaviors concentrated on the sole use, by navigating birds, of a single environmental cue, such as solar (Matthews, 1953; Pennycuick, 1960) or magnetic (Yeagley, 1947, 1951) cues. Most current research, however, focuses upon the probable use of multiple cues by migrating and homing animals. Recent research has led to the discovery of unexpected sensory systems sensitive to magnetic fields, ultraviolet light, polarization patterns, infrasound and barometric pressure (reviewed in Able, 1980; Griffin, 1978; Kreithen, 1978). Although such important advances are continually being made, as evidenced by several recent symposia (Papi and Wallraff, 1982; Schmidt-Koenig and Keeton, 1978), much remains to be learned about orientation behavior.

A major portion of orientation research has dealt with insects (see von Frisch, 1967; Johnson, 1969) and birds (see Gauthreaux, 1980; Papi and Wallraff, 1982), most often with homing pigeons (reviewed in Schmidt-Koenig, 1983). While such studies have led to important discoveries concerning mechanisms of orientation, models used to explain bird navigation may not be applicable to the shorter range homing performed by small terrestrial vertebrates. Such animals do not generally travel the great distances traversed by many birds and it is therefore possible to observe their natural movements in field situations. Studies on such easily observed animals could contribute significantly to a broader understanding of orientation mechanisms. Yet Able (1980), in his review of mechanisms of animal orientation, noted a lack of sufficient descriptive data to precisely define the orientation abilities of many terrestrial species, especially reptiles and mammals. Detailed, long-term studies of the orientation behavior of single species, followed by systematic experiments designed to reveal the underlying mechanisms of orientation, are necessary in order to gather such information.

Except for the research on birds discussed above, the only other major vertebrate taxonomic group whose orientation has been extensively studied in such a manner is the Amphibia. Reptiles and mammals have rarely been investigated, although recent studies have added to our understanding of the mechanisms of orientation of a few species (wood turtles, *Clemmys insculpta* (Barzilay, 1980), painted turtles, *Chrysemys picta* (DeRosa and Taylor, 1978, 1982), spiny softshell turtles, *Trionyx spinifer* and Eastern box turtles, *Terrapene carolina* (DeRosa and Taylor, 1982), American alligators, *Alligator mississippiensis* (Murphy, 1981) and white-footed mice, *Peromyscus leucopus noveboracensis* (Cooke and Terman, 1977; Parsons and Terman, 1978). Considerably more research must be done, however, before it can be said that there is a generally broad, taxonomic coverage of research in the area of animal orientation.

The primary purpose of the present study was to investigate the homing ability of a single species of lizard, *Sceloporus jarrovi*, followed by studies of the various mechanisms important in this behavior. A review of previous homing studies involving lizards, as well as a discussion of the role of extraoptic photoreceptors in amphibian orientation and saurian behavior, is given to provide a basis for interpretation of this study.

A. Review of Homing Behavior in Lizards

Although there have been many studies of homing in vertebrates, few exist for lizards. Most reports of a homing ability in lizards have been anecdotal, generally included in more comprehensive studies of the general ecology and demography of the species. Successful homing after displacement has been reported for the eastern fence lizard, Sceloporus undulatus, from distances up to 274 m (Noble, 1934); for the granite spiny lizard, Sceloporus orcutti, from up to 150 m (Mayhew, 1963); and for the side-blotched lizard, Uta stansburiana, from distances of 49-122 m (Spoecker, 1967). Fitch (1940) found no indication of a homing ability for western fence lizards, Sceloporus occidentalis, which were displaced a "few hundred yards". Negative results have also been reported for Uta stansburiana displaced approximately 91 m from their capture point (Tinkle, 1967) and for one tropical anole, Anolis lineatopus, displaced 180 m (Rand, 1967).

Several recent studies have carefully documented the ability of lizards to return to their home areas after deliberate displacement. Weintraub (1970) displaced over 230 individual Sceloporus orcutti and found that adult males could return with good success from distances up to 215 m. Data from 11 adult males indicated that the movement back to the capture point was direct and fairly rapid. Reciprocal displacements between two areas ruled out any possible stereotyped movement patterns. He found that lizards homed better from areas in which the capture point was visible than from areas hidden from this point. His conclusion was that these lizards probably use Type I homing (Griffin, 1952), in which familiar landmarks determine movement.

Krekorian (1977) recently investigated the homing ability of iguanas, Dipsosaurus dorsalis. Lizards were displaced distances ranging from 50-400 m in an open, level habitat. Of the 83 lizards displaced, 22 successfully homed at least once from a maximum distance of 274 m. Four lizards were observed moving in a direct path toward their capture points.

Guyer (1978) studied the homing orientation of the short-horned lizard, Phrynosoma douglassi, and the sagebrush lizard, Sceloporus graciosus. Three of 31 displaced Phrynosoma douglassi returned home from distances up to 148 m. Sixteen of 58 adult Sceloporus graciosus homed successfully while only five of 51 juveniles returned to their original capture sites. The longest return for Sceloporus graciosus was 280 m by a juvenile male. The return success was inversely related to distance displaced. In addition, both species were able to orient in a homeward direction after displacement as indicated by Rayleigh V-tests (Batschelet, 1965, 1972).

In two of the studies of lizard homing described above (Weintraub, 1970; Krekorian, 1977) the success rate seemed to be dependent on the home area being visible at the displacement site. Both of these studies were done in relatively open habitats where a lizard could have a clear field of vision for hundreds of meters. In the study by Guyer (1978) it is unclear whether lizards would have had a clear view of their home areas from the displacement site. It is unlikely, however, since lizards were released in an area characterized by rolling hills with widely spaced sagebrush.

Ishihara (1969) studied the homing behavior of the Oriental grass lizard, Takydromus tachydromoides (Schlegel). These lacertid lizards inhabit the grasslands of Southeast Asia, a habitat where long-distance views would be severely restricted. The maximum distance from which these lizards homed was 180 m. The average time required for covering this distance was three days. For this species a direct field of vision back to the home area does not appear to be necessary for homing.

The above review documents homing ability in four North American iguanid lizards as well as in one Southeast Asian lacertid. The only analysis to date of a lizard homing mechanism is Weintraub's (1970) study of _Sceloporus orcutti_. He attempted to analyze the orientation of these lizards to the sun but found that the animals oriented to the sun for thermoregulatory functions, not for homing.

The orientational mechanisms underlying lizard homing ability have been completely unknown. However, numerous studies on the mechanisms of homing and orientation have been conducted on amphibians. A review of the amphibian literature shows the wide range of sensory modalities that can be utilized for orientation. Information on sensory involvement in homing orientation has been obtained mainly by manipulating the experimental subject, either by sensory impairment, conditioning procedures, or circadian rhythm alterations. Such techniques can also be utilized to study saurian orientation mechanisms. A review of orientation mechanisms, with emphasis on amphibian research, follows.

B. Sensory Mechanisms in Terrestrial Vertebrate Orientation

There is abundant evidence of the existence of celestial or sun-compass orientation in many groups of amphibians including frogs, toads, newts and other salamanders (Ferguson, 1967; Ferguson _et al_, 1968; Landreth and Ferguson, 1967, 1968; Taylor and Ferguson, 1970).

These experiments show that amphibians can use celestial cues to orient correctly on a compass course.

Sun-compass orientation requires three sources of information: a useful celestial cue, an intrinsic biological clock mechanism synchronized with local time, and a learned compass direction such as a shoreline or home territory. An internal clock is essential for this type of orientation since the position of the sun, or any other constantly-moving celestial cue, is predictable and dependable as a reference only if the animal knows the time of day.

A powerful technique for studying the role of an internal clock in compass orientation is the so-called clock-shift experiment. Such experiments involve re-setting of the animals' internal clock to a cycle out of phase with the natural day-night cycle. These phase-shifts result in predictable shifts in the direction of orientation. For example, a six hour phase advance (one quarter of a daily cycle) results in a 90° counterclockwise shift (one quarter of a circle) in orientation if animals are compensating for the movement of the sun. Experiments of this type are used to demonstrate time-dependence and imply the use of celestial cues (reviewed in Adler, 1976; Keeton, 1974).

Sun-compass orientation is well documented in birds (reviewed in Keeton, 1974) and has recently been demonstrated in a few species of reptiles: water snakes, *Nerodia sipedon* and *Regina septemvittata* (Newcomer, Taylor and Guttman, 1974); turtles, *Chrysemys picta*, *Trionyx spinifer* and *Terrapene carolina* (DeRosa and Taylor, 1978, 1982); and alligators (*Alligator mississippiensis* (Murphy, 1981).

Fischer (1961) studied the orientation of the lacertid lizard, *Lacerta viridis*, under both natural skies and an artificial sun. He determined that the lizards possessed a timing mechanism which was in synchrony with the movement of the artificial sun. Phase-shifted lizards deviated in the predicted manner from the trained direction. Experiments on lizards trained and tested under natural skies produced similar results which suggest that the animals were able to use celestial cues in goal finding.

Homing of blind amphibians has been authenticated in numerous reports (Dole, 1968; Grubb, 1970; Oldham, 1967; Tracy and Dole, 1969; Twitty, 1959). Some investigators have attributed the homing of blind amphibians to the use of olfactory cues (Dole, 1968; Oldham, 1967; Twitty, 1959; Twitty *et al*, 1967; Madison, 1969). The results of most of these experiments can be explained by an alternative hypothesis that assumes an extraocular photoreceptor (EOP) mechanism which will be described in more detail below. There is evidence, however, that olfactory cues do supply useful orientation information for salamanders (Grant *et al*, 1968; Madison, 1969, 1972; Madison and Shoop, 1970; Barthalmus and Bellis, 1972) and some frogs and toads (Martof, 1962; Oldham, 1967; Dole, 1968; Tracy and Dole, 1969; Grubb, 1970).

During the past 15 years it has been demonstrated that amphibians are able to use extraoptic photoreceptors (EOP's) for orientation (Landreth and Ferguson, 1967; Taylor and Ferguson, 1970; Adler and Taylor, 1973). These studies showed that in salamanders (Taylor, 1972) and frogs (Taylor and Ferguson, 1970) eyeless animals retain the ability to use celestial cues for orientation while animals without eyes and with their brains covered with black plastic appear disoriented.

Endogenous circadian rhythms of both urodele (Adler, 1968, 1969) and anuran (Adler, 1971) amphibians can also be manipulated by light cues received extraoptically. Eyeless salamanders, Plethodon glutinosus, are able to phase-shift circadian locomotor rhythms in response to shifts in light-dark cycles (Adler, 1969). A more thorough review of amphibian rhythms and orientation can be found in Adler (1970, 1976).

Tests with eyeless salamanders, Ambystoma tigrinum, have shown that the pineal body can function as an effective EOP for compass orientation since the response is abolished by pinealectomy or by covering the pineal with opaque material (Taylor and Adler, 1978). Similar experiments on bullfrog tadpoles (Rana catesbeiana) investigated the role of the intracranial pineal body and the extracranial frontal organ in celestial orientation (Justis and Taylor, 1976). The results implicated both organs as effective EOPs in the orientation response. Additionally, Demian and Taylor (1977) demonstrated that eyeless newts, Notophthalmus viridescens, were able to synchronize their activity patterns to an imposed light cycle while animals without pineals did not entrain to the light cycle. These results indicate that the pineal complex is involved in both orientation behavior and in the entrainment of endogenous rhythms in amphibians.

It has been shown that tiger salamanders, Ambystoma tigrinum, can perceive the axis of linearly-polarized light and use it for purposes of orientation (Taylor and Adler, 1973). Such orientation behavior, a phenomenon termed polarotaxis (Waterman, 1966), has been shown to be dependent on a cranial EOP (Adler and Taylor, 1973). Of the groups of salamanders tested, only those animals with an opaque shield over the skull failed to orient to the plane of polarization, e-vector, of linearly-polarized light. These shielded animals failed to orient even when their eyes were fully intact and undisturbed.

Recent evidence indicates that both bullfrog tadpoles and red-spotted newts can perceive linearly-polarized light and use the polarization patterns in clear blue sky for compass orientation, even when the sun is not in view (Taylor and Auburn, 1978; Auburn and Taylor, 1979). These studies also indicate that the pineal complex is the probable receptor of linearly-polarized light.

C. The Pineal Complex in Lizards

The evidence presented above indicates a role of the pineal complex in amphibian orientation. The close phylogenetic relationship of amphibians and lizards, as well as similarities in their pineal systems, suggests that a similar function could exist in lizards.

Among living vertebrates lizards possess the most highly differentiated EOPs. The pineal complex consists of two separate photoreceptive organs in most lizards: the parietal eye and the pineal organ. While the pineal organ is present in all lizards, some species do not possess a parietal eye. The parietal eye is thought to be homologous to the frog's frontal organ (Ariëns-Kappers, 1965). Both the pineal organ and the parietal eye are derived embryologically as evaginations of the roof of the diencephalon (Wurtman, Axelrod and Kelly, 1968).

Neurophysiological and ultrastructural studies have shown that in all lizards studied the parietal eye is a functional photoreceptor (reviewed in Eakin, 1973). The parietal eye frequently contains a well-developed cornea, a lens, and a retina. Early anatomical studies of the parietal eye demonstrated that the retina contains photosensory cells similar in appearance to those found in the lateral eyes (Eakin and Westfall, 1959, 1960; Steyn, 1959, 1960; Eakin, Quay and Westfall, 1961).

The retina is composed of three distinct layers: 1) a central ganglion layer, 2) a distal layer of photoreceptors and 3) an intermediate plexiform layer (Jenison and Nolte, 1979). Horizontal sections of the parietal eye show the outer segments of the photoreceptors arranged in a centrally-projecting pattern where many are in a plane perpendicular to overhead light (Hamasaki and Eder, 1977). Such an arrangement would theoretically allow for analysis of polarized light (for discussion see Adler and Taylor, 1973).

Jenison, Eldred and Nolte (1979) have recently discovered a new population of neurons, termed photoreceptor-nuclear-layer neurons (PNL), within the distal layer of the parietal retinas of two iguanid lizards, Iguana iguana and Anolis carolinensis. They suggest these PNL neurons may act as interneurons between the photoreceptors and the ganglion cells. This may indicate a more complex processing of photosensory information than was previously assumed when the only neural connections known to exist were between the ganglion cells and the photoreceptors. The parietal eye has a well-developed nerve which contains both afferent and efferent fibers (Engbretson and Lent, 1976). The eye responds to illumination by sending afferent impulses to the pineal gland during daylight hours. A feedback system exists in which efferent neurons sensitive to norepinephrine conduct impulses back to the parietal eye, enhancing photoresponsiveness.

Chromatic responses to light have been recorded from both the parietal eye (Miller and Wolbarsht, 1962; Dodt and Scherer, 1968; Hamasaki, 1968) and the pineal organ (Hamasaki and Dodt, 1969). The photic response to all wavelengths of light by the pineal organ is purely inhibitory, with a maximum sensitivity at about 600 nm (Hamasaki and Dodt, 1969). Electrical properties are more complex in the parietal eye. Visible light of shorter wavelengths tends to inhibit electrical activity whereas visible light of longer wavelengths stimulates electrical activity (Dodt and Scherer, 1968; Hamasaki, 1969a, b; Hamasaki and Eder, 1977).

The high degree of organization in the retinas of both the parietal eye and the lateral eye is not observed in the pineal organ (reviewed in Eakin, 1973). Many cells in the pineal organ of lizards show characteristics of photoreceptors (Collin, 1971; Oksche, 1971) while other cells seem to be modified or rudimentary in appearance (Collin, 1971).

The above review indicates that the parietal eye is a more highly-differentiated optic apparatus than the lizard pineal organ. It also appears to be more specialized than the light-sensitive frontal and pineal organs in Amphibia (Adler, 1976) which have already been shown to be important in orientation behavior. Therefore, it is quite possible that the parietal eye of lizards could be useful in orientation.

The function of the parietal eye in mediating such light-dependent processes as reproduction, activity and thermoregulation has been studied by many workers (reviewed in Eakin, 1973; Ralph _et al_, 1979). Stebbins and co-workers have done extensive work on the possible role of the parietal eye as a radiation dosimeter (Glaser, 1958; Stebbins and Eakin, 1958; Stebbins, 1960, 1963; Stebbins and Wilhoft, 1966; Stebbins and Cohen, 1973). They observed that parietalectomized, or parietal shielded, lizards spent more time exposed to sunlight. In addition, these lizards displayed increased locomotor activity and traveled greater distances than sham-operated controls. These researchers concluded that the parietal eye functions as a dosimeter for solar radiation, helping to synchronize the daily and seasonal activity and reproductive cycles of the lizards with the photic environment. Hamasaki and Eder (1977), however, suggested that these results could be as easily explained if the parietal eye functioned in the daily orientational responses of the lizards. Without the necessary orientational cues from the parietal eye lizards might become disoriented and tend to remain on the surface longer and wander further than normal.

As noted earlier, EOPs have been found to entrain circadian activity rhythms to the prevailing light cycle in amphibians. The pineal organ has been implicated in this response. Removal of the pineal organ and parietal eye in blinded lizards, however, did not prevent entrainment (Underwood and Menaker, 1970; Underwood, 1973; Underwood and Menaker, 1976). However, a more subtle influence of the pineal complex on circadian activity in lizards has since been shown (Underwood, 1977). The free-running circadian rhythm of Texas spiny lizards, Sceloporus olivaceus, was studied under continuous illumination. Removal of the parietal eye alone had no effect on the free-running activity rhythm of any lizard. Subsequent removal of the pineal organ, however, had significant effects: 1) a marked change in the period of the free-running rhythm, or 2) arrhythmicity (constant activity with no discernible period). Simultaneous removal of both the parietal eye and the pineal organ led to an additional effect: a "splitting" of the circadian activity rhythm into two components. Underwood (1977) suggests that these effects are consistent with either of two hypotheses: 1) the pineal organ acts as a coupling device between two or more circadian oscillators, or 2) the pineal organ is a master oscillator which entrains other circadian oscillators.

Recent experiments indicate that the parietal eye may play a role in the behavioral thermoregulation of lizards (Kosh and Hutchison, 1972; Hutchison and Kosh, 1974; Engbretson and Hutchison, 1976; Ralph, Firth and Turner, 1979; Ralph et al, 1979). When allowed to behaviorally select body temperatures in laboratory thermal gradients, parietalectomized lizards tend to select warmer temperatures than controls. These results are obtained even in the absence of a photic gradient (Hutchison and Kosh, 1974; Engbretson and Hutchison, 1976; Roth and Ralph, 1977; Phillips and Harlow, 1981). These workers suggest that the parietal eye may transmit both photic and thermal information to the brain centers involved in the modulation of thermoregulatory behavior.

Recent research on horned lizards, Phrynosoma douglassi, suggests that this selection of higher temperatures by parietalectomized lizards may be controlled by hormonal rather than neuronal mechanisms (Phillips and Harlow, 1981). Lizards with the parietal eye shielded retreated from hot substrates ($48 \pm 3^{\circ}C$) at higher body temperatures than controls. Subsequent removal of the shield led to a lowering of these retreat temperatures to the level of the control group. There was, however, a four to six day lag observed in both the elevation and lowering of retreat body temperature. Glaser (1958) also noted a delay in the increased locomotor activity of night lizards, Xantusia vigilis, after shielding the parietal eye. Since the parietal eye is structurally and functionally associated with the pineal organ, Phillips and Harlow (1981) suggest that changes in the level of the hormone, melatonin, might be causing the shifts in thermoregulation and behavior. A study by Firth and Kennaway (1980) supports this possibility. Removal of the parietal eye abolished the diurnal rhythm in plasma melatonin while shielding the lateral eyes had no effect. Taken together these results are consistent with a hypothesis that the parietal eye/pineal complex is partially mediating lizard body temperatures through its control of melatonin levels.

Parietalectomy of lizards has been demonstrated to alter numerous biological functions such as activity patterns (Glaser, 1958; Firth, 1974; Engbretson and Hutchison, 1976), seasonal reproductive and thyroid cycles (Stebbins, 1970; Stebbins and Cohen, 1973), metabolic rates (Songdahl and Hutchison, 1972), and the diel pattern of temperature selection (Hutchison and Kosh, 1974). These changes, however, may be indirect effects of the voluntary selection of higher body temperatures by parietalectomized lizards.

Such an indirect effect on reproductive cycles has recently been demonstrated in Anolis carolinensis (Underwood, 1981). The maintenance and subsequent regression of the anole testes in late summer has been shown to be controlled primarily by photoperiod (Licht, 1971). Prior studies have failed to show a convincing role of the parietal eye in such photoperiodic responses (Licht and Pearson, 1970; Underwood, 1975). These studies examined the anoles responses when exposed to constant temperatures. Underwood (1981) designed his study to examine the photoperiodic responses of parietalectomized anoles exposed to either a constant temperature regimen or to thermal gradients. When held at a constant 32°C parietalectomy did not affect testicular growth of the anoles. Parietalectomized anoles did, however, show significantly more testicular growth than the sham-operated controls when exposed to a thermal gradient. These results suggest that the parietal eye can affect a photoperiodic response, but the effect is an indirect one. That is, parietalectomy causes lizards to select higher body temperatures which, in turn, affects a photoperiodically dependent response such as testicular growth.

It would be wise, therefore, when studying any function of the parietal eye to always take into account the possible thermoregulatory disruptions caused by parietalectomy. For instance, the selection of higher body temperatures by parietalectomized lizards utilized in an orientation study could be the underlying cause of any disorientation later discovered. Thus it is necessary to either test the orientation behavior of control and experimental animals at constant temperatures or to simultaneously monitor the body temperatures of the tested animals to determine what effect there is on thermoregulation. The monitoring approach is the only one that would be feasible in field studies and is the one utilized in the present study.

D. Objectives

The purpose of this study was to investigate the homing behavior of a single species of lizard, Sceloporus jarrovi. The study had the following objectives:

1) To study the effect of age, sex and displacement distance on homing success.

2) To determine the effect of blocking the parietal eye on homing success and initial orientation towards home.

3) To successfully track the return pathways of homing lizards as well as the wanderings of non-homing lizards. Such information was used to distinguish between homing by random wandering and directed movement towards home.

4) To determine whether the initial orientation of *Sceloporus jarrovi* depends upon a celestial compass.

5) To do a field study of the effect of blocking the parietal eye on lizard thermoregulation.

II. METHODS

A. Study Site and General Methods

Sceloporus jarrovi occurs in the mountains of southern Arizona, southern New Mexico, and Mexico at elevations between 1500 and 2600 meters (Stebbins, 1954). These mountains, including the Chiricahua Mountains where the study was conducted, form islands of relatively moist habitats surrounded by desert and grassland.

Sceloporus jarrovi is locally abundant in rocky canyons and in other areas having rocky outcroppings. Field work was done in the South Fork of Cave Creek Canyon at an elevation of 1525 m, approximately 7 kilometers southwest of Portal, Arizona. The two hectare study area is located in riparian habitat in the bottom of a rocky canyon. Arizona sycamores (*Platanus wrightii*) border the ephemeral stream which flows through the midline of the study area during the rainy months of July and August. The surrounding area consists of an oak - pine association dominated by Arizona pine (*Pinus ponderosa* var. *arizonica*), oaks (*Quercus* sp.), Douglas fir (*Pseudotsuga menziesii*), and Arizona cypress (*Cupressus arizonica*).

Laboratory work was performed at The Southwestern Research Station of the American Museum of Natural History which is located approximately 5.0 km by road plus 1.0 km by trail from the study site in South Fork.

Field observations were made during the summers of 1978 through 1982 as well as during the spring of 1982. Each year an attempt was made to mark all *S. jarrovi* on the study site. Lizards were captured by noosing and then toe-clipped, marked with paint and released (as in

Tinkle, 1967). Upon capture sex, snout-vent length and weight were recorded. Animals were recaptured only after molting or for experimental manipulations.

Adults were animals that had overwintered at least once. Animals born in the current year, usually in May or June, were called juveniles. The exact ages of individual lizards could only be determined if the animal had been initially captured as a juvenile. Otherwise, ages of lizards first captured as adults were estimated from their size. The distribution of sizes of the lizards of known ages was the basis for these estimates (Bissinger, unpublished data).

A daily record was kept of all lizards sighted. The locations of individual animals were noted both in descriptive field notes and on a map of the study area (Figure 1).

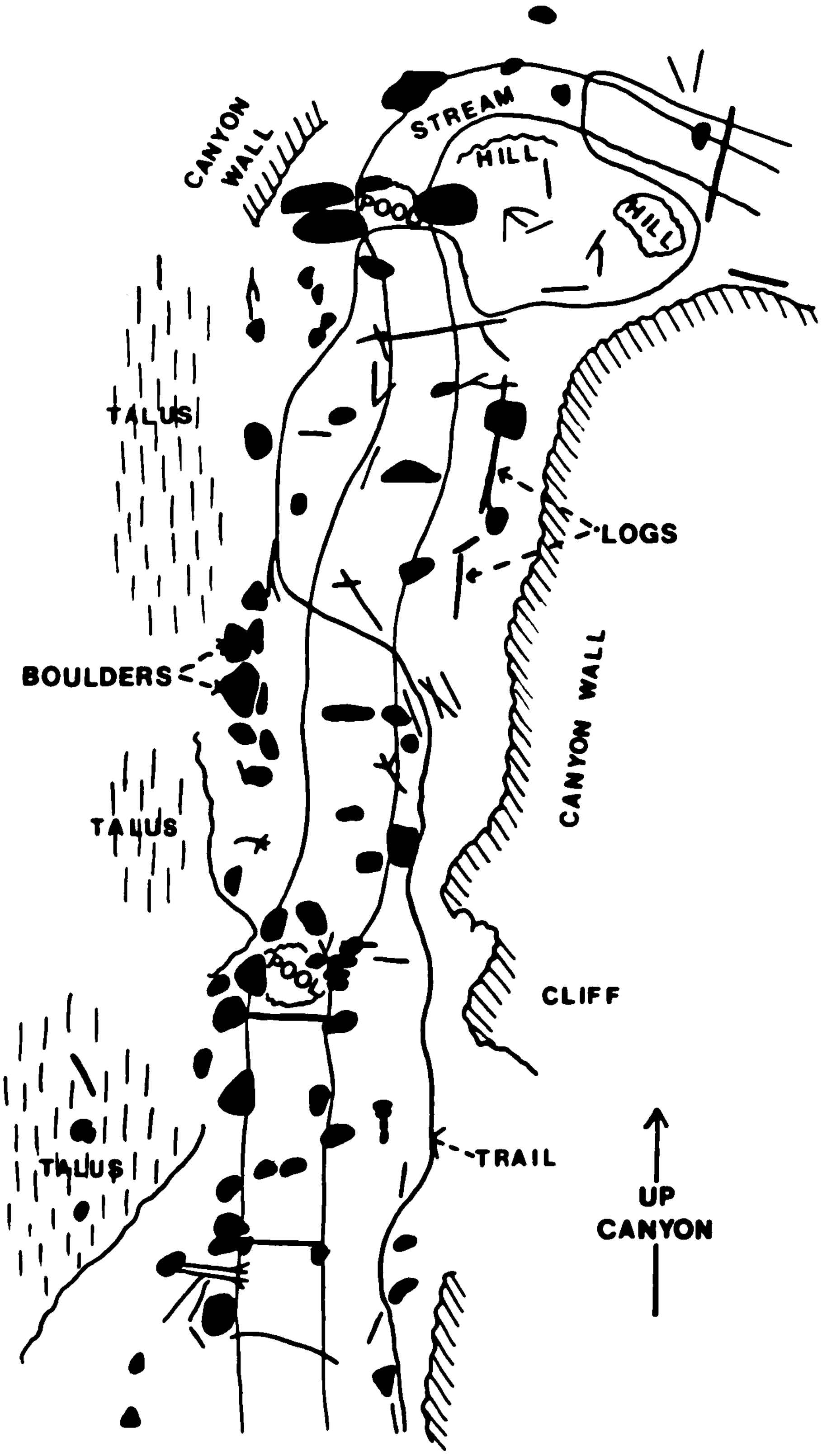
This project had five objectives. Procedures and manipulations for studying specific aspects of these objectives are given in the following sections. Details of specific statistical analyses are discussed in the appropriate sections. For all analyses, results were considered significant if the probability was five percent or less.

B. Homing Studies

Studies of the homing behavior of normal lizards were conducted during the summer of 1978. Homing, in this study, will refer to the ability of a lizard to return to its home area after artificial displacement.

Before individual lizards could be utilized in displacement experiments they had to be verified as residents of the study site. A transient animal, lacking a defined home area, would not be expected to return to its initial capture point after displacement. The month

Figure 1. Simplified version of field map of the study site.


CANYON WALL
STREAM
HILL
HILL
POOL
TALUS
LOGS
BOULDERS
CANYON WALL
TALUS
POOL
CLIFF
TALUS
TRAIL
UP CANYON

of July, 1978 was spent marking lizards and accumulating location data for all lizards sighted. A lizard was considered a resident if it met one of the following criteria: 1) was sighted at least three times, with all sightings within 15 m of one another, or 2) had lived in the same home area in previous years as determined from prior sighting records (Simon, unpublished data).

Knowledge of home range size is necessary in any homing study in order to be certain that animals are being displaced well outside the normal range of their movements. The home range size of four age-sex classes of lizards was determined: adult males, adult females, juvenile males and juvenile females and home ranges were mapped for seven resident lizards in each age-sex class.

Home range mapping followed the method of Simon (1976). A Polaroid photograph was taken of the location of the lizard. Thirty-minute observations of the activity of individual lizards were made through binoculars from a minimum distance of 10 m so as to avoid disturbing the animal. Each time the lizard moved its exact location was recorded on the photograph. If a lizard moved out of the range of the photograph another photo was taken to include the new area. A minimum of three 30-minute observations were necessary before a lizard's home range was considered to be completely mapped. Each map was based on 30 to 59 distinct locations. Since the scale was different in every photograph, individual home ranges were measured in the field using a measuring tape and compass while referring to the photographs.

The translation of the field data into a numeric estimate of the home range size poses a problem. Procedures available for such estimates can be divided into two general categories: polygons and probability density distributions. Polygon methods estimate the area containing all sightings of an animal and make no statistical assumptions about the distribution of sightings of animals in their home ranges. The second procedure, the probability density function, involves calculating statistical parameters of a theoretical distribution assumed to underlie the home range observations (Dice and Clark, 1953; Calhoun and Casby, 1958; Jennrich and Turner, 1969; Koepple, Slade and Hoffman, 1975). One probability density function, the recapture radius method, involves calculating the distance of individual sightings from the geometric center of all sightings. A standard radius can then be calculated and utilized to determine the length of a radius that is needed to enclose 95 percent of the sightings (Harrison, 1958; White, 1964).

Recapture radii estimates have been shown to over-estimate the home range of lizards when compared to polygon techniques (Waldschmidt, 1979; Rose, 1982). The principal differences in the estimates are due to the fact that the statistical method assigns a probability of finding an animal where that animal was never observed. Due to this fact, as well as due to violations of underlying assumptions, these statistical methods should probably be avoided in comparisons of home range sizes between populations of species or between species (Waldschmidt, 1979; Rose, 1982). Waldschmidt (1979), however, suggests that the recapture radii method may still be useful in describing the average movements within a population. As such it simply describes how far one can expect the average animal to move.

I decided to use the recapture radii method because it gives an approximation of the average distance traveled by a lizard, a value which can be directly compared to the displacement distances. Any over-estimate of the home range radius would be consistent between age-sex classes or experimental groups. In addition, it is preferable to over-estimate rather than under-estimate the home range index of the area familiar to an animal since when testing homing mechanisms it is imperative to displace the animals outside of their area of familiarity.

Displacements of lizards took place during August, 1978. Thirty-nine adults and 31 juvenile lizards were displaced at least once; one adult male was displaced twice. Each lizard was placed within a plastic bag that went into a heavy cloth bag and carried a predetermined distance to its release point. Flagging tied onto trees indicated the release point. Displacement distances ranged from 50 to 200 m. No juveniles were displaced 200 m due to the low homing success of this group at shorter distances. Approximately equal numbers of lizards were displaced up the canyon (South) as well as down the canyon (North). Successful homing was indicated by the return of a lizard to within 10 m of its initial capture point or another previous sighting location by the end of the summer.

C. Parietal Eye and Homing

1. Displacement Studies - Field observations were performed on adult lizards in June and July, 1979 and in July and August of 1980. Every lizard used was verified to be a resident of the area prior to any manipulations.

The project consisted of displacements of three test groups of lizards: 1) Normal (N) animals (18♂, 20♀) were released without further treatment. 2) Sham-treated (S) lizards (18♂, 17♀) had paint placed alongside the parietal eye. 3) Experimental (E) lizards (20♂, 20♀) had the parietal eye and surrounding parietal scale covered with a thick layer of paint. Captured lizards were randomly assigned to groups, placed in opaque bags and then displaced approximately 150 m. Additional lizards, the controls, were captured, treated with one of the three manipulations (N: 9♂, 11♀; S: 17♂, 16♀; or E: 17♂, 19♀), and immediately returned to their home areas. The purpose of the control groups was to determine the effect of the parietal eye manipulations on lizard activity, survivorship, and home range size.

At the end of the field season home range recapture radii of the control animals were calculated from the daily sighting records. In addition, survivorship of both the control and displaced animals was calculated from these daily records. Survivorship was calculated by two different methods. Animals were considered to be survivors if: 1) they were sighted on the seventh or any subsequent day after their initial treatment, or 2) were sighted in any subsequent year.

2. Radio-tracking studies - Research on the homing behavior of male lizards was performed during May, 1982. All displacements of females were postponed until after the young were born in June. S. jarrovi is a viviparous species with young being born in early summer (Goldberg, 1971; Ballinger, 1973, 1979).

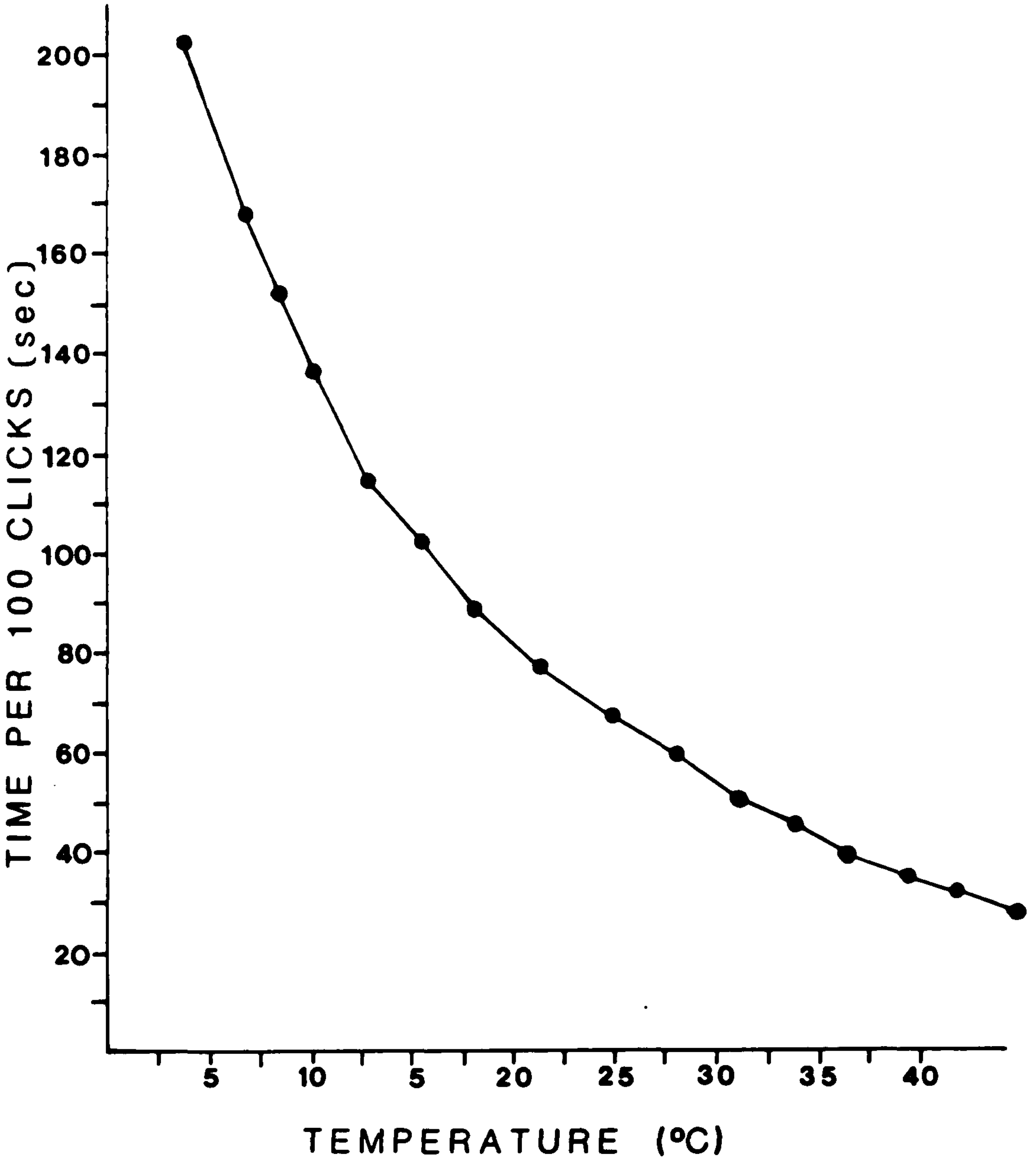
All radio-tracking equipment utilized in these studies was designed and supplied by The Mini-Mitter Co., Inc., Sunriver, Oregon. The transmitters used were the Model T, powered by a 1.35 volt MS-13 mercury battery. Each transmitter was encased in heat-shrink tubing and then dipped into Parafin/Elvax to provide a waterproof coating. The resulting package was a cylinder measuring 20 mm x 7 mm and weighing 2.1 g. Each transmitter produced a unique signal lying between 27.555 and 27.615 MHz. This signal could be received from 20 to 30 m away, depending on transmitter orientation and local topography.

The temperature-sensitive transmitters were calibrated in a water bath at increments of 2 to 4 Celsius degrees between 4°C and 45°C. The click rate of the transmitters increased with temperature. The amount of time (sec) for 100 clicks of the transmitter was measured for three consecutive periods, which were then averaged to obtain the calibration point at a given temperature. In all transmitters used the click rate was related to temperature in a non-linear fashion (Figure 2).

Lizards chosen for radio-tracking were all at least two years of age. This was necessary to insure that the animals were large enough to easily carry the size and weight of the transmitters. Males utilized in the study ranged in snout-vent (S-V) length from 75 to 94 mm and in weight from 15.7 to 25.6 g. Females studied were smaller, ranging from 71 to 81 mm in S-V length and 11.5 to 17.5 g. Thus, the transmitter/body weight ratio ranged from 8 to 18 percent.

The transmitters were surgically implanted in the abdominal cavity of each lizard. Animals were anesthetized by immobilizing them in a freezer for 5 to 10 minutes. Every few minutes they were checked for responsiveness. When a lizard no longer moved when prodded it was removed from the freezer, placed on its back on top of a tray of ice and then covered with an ice pack. Sterile instruments and clean

Figure 2. Temperature calibration curve for Transmitter F2.


200
180
160
140
120
100
80
60
40
20
TIME PER 100 CLICKS (sec)
5
10
5
20
25
30
35
40
TEMPERATURE (°C)

surgical gloves were used. An abdominal incision through the skin, musculature and peritoneum was made with a surgical blade and scissors. The incision ran parallel to and at least 0.5 cm away from the midline for a total length of about 1.0 cm. The encapsulated transmitter was placed in a 70 percent alcohol solution before being inserted into the abdominal cavity. Four sutures were usually required to close the incision. The suture material was Ethicon Mersilene 5-0 with an FS-3 needle.

Following surgery each lizard was slowly warmed up by placing it on my arm and covering it with a hand. When the animal began to move and became conscious of its surroundings it was returned to a clean aquarium in the laboratory. Each aquarium was provided with a heat lamp at one end to allow the lizard to raise its body temperature back to normal. Water and food, crickets and other insects, were provided to all animals. The behavior and body temperatures of all animals were checked frequently following surgery.

Lizards were returned to the field the next morning. Procedures differed slightly for the release of male and female lizards. Males were returned to the area of their home range and released. They were then radio-tracked within their home ranges for two days. This was done for two reasons: 1) to assess the effect of surgery and transmitter implantation on lizard behavior, and 2) to monitor body temperatures. Details concerning the thermoregulation study will follow in Section E. At the end of the second day after their release the males were recaptured and then displaced approximately 150 m via circuitous routes. Due to a shortage of time females were not returned to their home ranges following implantation. Instead they were simply displaced to a location 150 m from their known home range. Displaced animals were radio-tracked for two days, then recaptured and returned to the lab for removal of transmitters. Following the removal of transmitters all lizards were returned to their previous home ranges.

One Model CH-6 receiver with a Model AF antenna was used to determine a lizard's location by triangulation. Once the transmitter location was fixed an attempt was made to sight the lizard visually. Every day that a radio-implanted lizard was in the field its location was determined at intervals of approximately 30 minutes between the hours of 1000 and 1630.

Transmitters were implanted in three groups of animals for each sex: 1) normal, 2) sham, and 3) experimental. Since the receiver could simultaneously monitor six transmitters there were usually six lizards being tracked at one time, 2 from each treatment group. For the sham and experimental groups, paint was applied to the lizard's head immediately before its release in the field. Immediately following the release of an individual at its displacement site I left the area and did not return for approximately 30 minutes. This was done to avoid disturbing the lizard and possibly interfering with its direction of travel. Care was also taken to remain as far away from the individual as possible whenever obtaining radio fixes and visual sightings.

Data for 24 males (8 normal, 8 sham, 8 experimental), both within their home ranges and after displacement, were collected. Eighteen females (6 in each treatment group) were tracked following displacement. Thus, a total of 42 tracks were observed and recorded on field maps. The individual paths of displaced animals were mapped at the end of each phase (May or August) of the study. The maps consisted of segments between the half-hourly sightings. The direction of each segment was measured by placing the center of a compass on top of a sighting point and measuring the azimuth to the next sighting. This procedure was followed until the pathway of every lizard was recorded.

The Hodges-Anje test (Batschelet, 1972) was used to determine whether the travel paths of individual lizards were non-random. The component unit vectors of the travel paths are utilized in this test, which is sensitive to directions of vectors but not to their lengths. The null hypothesis, whether the directions comprising the lizard's path are uniform, is tested against the alternative hypothesis, that the distribution is not uniform. The angles are plotted on a unit circle and then a line is drawn to minimize the number of observations on one side of the line. This minimum number is the test statistic, k. If k is small enough compared with the sample size, the null hypothesis can be rejected. While rejection of the null hypothesis does not directly test the track orientation, it does imply that the animals were traveling on an oriented pathway.

The Hotelling One-Sample T^2 test (Batschelet, 1978), a second-order analysis, was used to determine whether the tracks of lizards within each treatment group were oriented towards home. In this test, the question of whether a group of animals shows an orientation toward a common direction reduces to another question: whether the center of a scatter diagram of vectors differs from a reference point, such as 0. This involves calculation of a confidence ellipse and is based on a bivariate normal distribution. If the confidence ellipse covers the origin, a concentration of vectors around a certain direction cannot be shown. However, if the confidence ellipse does not cover the origin, the vectors are shown to be significantly concentrated around a common direction.

In addition, the initial orientation of the groups of lizards was tested. The angles from the release point to the first sighting 30 minutes later were analyzed by the Rayleigh test (Batschelet, 1965) to determine if orientation was uniform or non-uniform. The V test (Batschelet, 1972) was used to determine whether the lizards were significantly oriented in the homeward direction.

D. Parietal Eye and Sun-compass Orientation

This study, done during July and August, 1982, used only resident adult males which were at least two years of age. Lizards were captured on the study site, brought to the laboratory, and then placed in one of two separate environmental chambers. One chamber maintained a photoperiod regime which approximated the natural day-night cycle (LD 13:11; lights on at 0600 MST and off at 1900). The other chamber maintained a light-dark cycle that was advanced six hours as compared with the first chamber as well as to ambient conditions (LD 13:11; lights on at midnight and off at 1300). Such a phase-shift should result in an approximate 90° counter-clockwise shift in orientation if the animals are using a time-compensated celestial compass. Both environmental chambers also maintained a daily temperature cycle with the minimum temperature of about $15^\circ C$ occurring near the end of the dark phase and the maximum temperature of $40^\circ C$ occurring under the light source several hours after lights on. Lizards remained in the environmental chambers for at least seven days during which time they received fresh water and food once a day during the light phase. Twenty lizards were subjected to the advanced phase-shift while 20 others were maintained on the natural cycle.

On the day preceding its return to the field each lizard had a transmitter surgically implanted. This was done during the light phase of the daily cycle so as not to interfere with the phase-shifting process, as well as to allow the animal to regain its body temperature following surgery by basking under the lights in the chamber.

Four lizards were returned to the field at approximately 0900 on each day of release, two from each environmental chamber. Immediately prior to the release in the field one lizard from each phase-shift group had paint placed over the parietal eye and surrounding parietal scale while the other remained unpainted. Thus, the four treatments were: 1) normal lizards: no phase-shift (NPS), 2) normal lizards: advanced phase-shift (APS), 3) experimental lizards: NPS, and 4) experimental lizards: APS. All lizards were released at a displacement location 150 m away from their home ranges. Radio-locations were determined for each lizard at 30 minute intervals until early afternoon. Lizards were then captured and returned to SWRS for removal of transmitters. Following surgery, they were returned to the field and released in their original home ranges.

The initial orientation of the lizards was analyzed with Rayleigh tests to determine whether the lizards within a treatment group were significantly oriented and with V tests to determine whether they were oriented towards home. In addition, the non-parametric Watson's U^2 test (Batschelet, 1965) was used to determine if the orientation of pairs of treatment groups was significantly different.

E. Parietal Eye and Thermoregulation

The thermoregulation studies were done concurrently with the radio-tracking studies described previously in section C-2. During May, 1982 the thermoregulation of 24 adult male lizards (8 individuals in each of the three parietal eye treatment groups: N, S, or E) was investigated. For three consecutive days lizard body temperatures were recorded at 30 minute intervals from the hours of 1000 to 1430. These hours were chosen to insure that all lizards had equal opportunity to thermoregulate. During these hours the sun was shining on all locations in the study site. Before 1000 and after 1430 unequally distributed areas were in shade due to blockage of the sun's rays by the canyon walls. Lizards were residing in their home ranges for the first two days of measurements. On the third day they were displaced into an unfamiliar area for the homing studies previously described. The thermoregulation of female S. jarrovi was investigated in August, 1982 in a slightly different manner. Following implantation of transmitters, 18 female lizards (6 in each treatment group) were returned to the field 150 m from their home areas. Body temperatures were then recorded for two days as they attempted to return home.

The body temperatures of individual lizards were indirectly recorded in the field by measuring, with a stopwatch, the time required for 100 clicks of the transmitter. These data were later converted to body temperatures by referring to the calibration curve for the individual transmitter.

An analysis of variance for one grouping factor (effect of parietal eye treatment) and two trial factors (time of day and number of days) was performed on the body temperature data using the BMDP

P2V computer program. This was followed by one-way analyses of variance and Student-Newman-Keuls (S-N-K) tests where appropriate.

III. RESULTS

A. Homing Studies

In this section I present the results from all the experiments conducted on normal lizards, i.e. those that had no parietal eye treatment. Thus, all lizards used in 1978 are included as well as those normal animals studied in 1979 and 1980.

1. Home Range and Seasonal Movements - 95 percent recapture radii were measured for a total of 48 lizards during the three summers (34 adults, 14 juveniles) although juveniles were studied only during 1978. Recapture radii ranged from 1.78 m for a juvenile male to 27.03 m for an adult female. Means for the four age-sex groups are presented in Table 1. A two-way analysis of variance found no significant difference between the sexes but did show a significant effect of age (Table 2). Two-sample t-tests indicated that juvenile females had significantly smaller recapture radii than adult females ($t = 2.08$, $df = 22$, $p < .05$) while in males there was no significant difference ($t = 1.69$, $df = 22$, $p > .10$).

The annual migration of S. jarrovi from their winter sites to their summer home ranges was observed during the spring of 1982. In the South Fork study area the winter sites are located in exposed rocky locations high up the canyon walls. During March and April, 1982 the lizards were especially abundant on the talus slopes located on the east canyon wall. In May, 1982 lizards moved perpendicular to the length of the canyon to reach their summer home ranges. During the 1982 field season both the winter and summer home areas were recorded for over 100 lizards (Bissinger, unpublished data). The summer home

TABLE 1. 95 percent recapture radii in meters for four age-sex classes. Mean ($\bar{X}$), standard error (SE), and sample size (N) are given.

Age-Sex Class	$\bar{X}$	SE	N
Males			
Adults	10.29	0.97	17
Juveniles	7.05	1.85	7
Females			
Adults	11.66	1.53	17
Juveniles	6.66	1.06	7

TABLE 2. Two-way ANOVA on normal lizard recapture radii.

Source	df	Mean Square	F	Probability
Sex	1	8.670	0.352	$>.50$
Age	1	168.426	6.838	$<.025$
Sex X Age	1	7.706	0.313	$>.50$
Error	44	24.630		

ranges of all such lizards were located in the canyon bottom almost immediately below their winter sites. All lizards moved down the canyon slopes to the lower elevations and then moved throughout the canyon bottom until reaching their previous summer home range or establishing a new one. In no case did a lizard move parallel to the canyon walls a distance greater than 30 m before settling into a summer home range.

2. Homing Behavior - Figure 3 shows the 1978 return success for adult and juvenile lizards displaced 50 to 200 m. Although each lizard was usually displaced only once, one adult male which returned home was then displaced in the opposite direction and is also included in the sample. Adult homing success from displacement distances up to 150 m was consistently high (72.7% to 81.8%) while it dropped considerably at 200 m (33.3%). This effect of displacement distance, however, was not shown to be significant ($X^2 = 4.668$, df = 3, $p > .10$). Juvenile homing success decreased significantly at distances greater than 50 m ($X^2 = 9.228$, df = 2, $p < .01$). Adults and juveniles had similar return success at the 50 m displacement distance ($X^2 = .005$, df = 1, $p > .90$). Juvenile return success at 100 m, however, was significantly lower than adults ($X^2 = 8.13$, df = 1, $p < .005$) with only one juvenile returning home. No juveniles successfully homed from 150 m, a result significantly lower than adult success ($X^2 = 8.869$, df = 1, $p < .005$).

The homing success of males and females over the three years was similar at all displacement distances (Table 3). Thus, male and female data are combined in all subsequent analyses.

Within adult lizards homing success was also affected by age. Analysis of the 150 m displacement data (the only displacement distance with a sufficiently large sample size for analysis) indicated that

Figure 3. Percent return success versus distance displaced for *Sceloporus jarrovi* adults and juveniles. Sample sizes appear over data points.

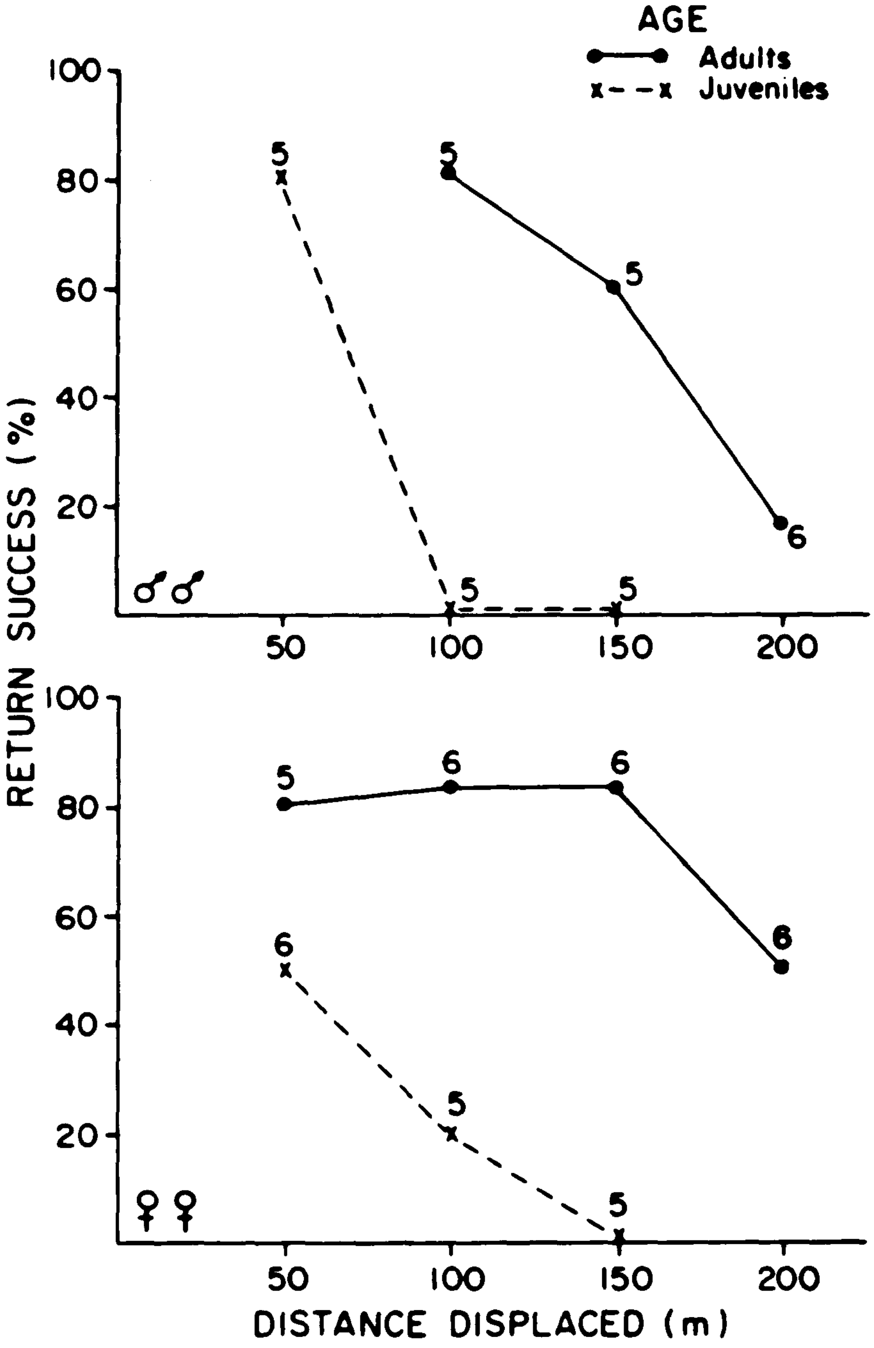

AGE
●—● Adults
x- -x Juveniles
RETURN SUCCESS (%)
100
80
60
40
20
♂♂
5
5
5
6
5
5
50
100
150
200
100
80
60
40
20
♀♀
5
6
6
6
6
5
5
50
100
150
200
DISTANCE DISPLACED (m)

TABLE 3. Effect of lizard gender on homing success. The table indicates the number of lizards that returned home and the number that did not home at three displacement distances.

	Males		Females				
Distance (m)	Home	Not Home	Home	Not Home	X^2	df	p
100	4	1	5	1	.414	1	$>.50$
150	15	7	16	10	.230	1	$>.50$
200	1	5	3	3	.889	1	$>.10$

one-year old adult lizards had a significantly lower homing success than older lizards (Table 4). One hundred percent of three-year or older lizards returned home, although this is not significantly different from the two-year old success (Table 4). Taken together these results suggest that homing ability increases with lizard age.

The time spent by lizards in returning to their home areas is not precisely known. However, the time between displacement and sighting in the home range was determined. These homing times ranged from 1 to 44 days. It is likely, however, that many lizards of all age classes returned home within a few days but were not immediately sighted. There was no correlation between the amount of time taken to return home and the displacement distance for lizards two years of age or older ($r = .258$, $df = 29$, $p > .05$). A significant correlation was found, however, in one-year old lizards ($r = .508$, $df = 14$, $p < .05$) indicating slower homing from longer distances. At the same time there was no correlation between lizard age and the amount of time taken to return home for two displacement distances (100 m : $r = -.167$, $df = 7$, $p > .05$; 150 m : $r = .107$, $df = 29$, $p > .05$).

There was no difference in homing success between male lizards displaced up the canyon (South) and those displaced down the canyon (North) (Table 5). One adult male was displaced twice in opposite directions and returned home both times. There did appear to be some effect of direction of displacement on the homing success of female S. jarrovi, although Chi-square tests were not significant. Only 45% of the females displaced down the canyon returned home as compared to 76% of those displaced in the opposite direction.

Twenty-six of the 108 lizards that were displaced were never

TABLE 4. Effect of lizard age on homing success at 150 m.

Comparison	Age	Home	Not Home	X^2	df	p
1)	1 year	10	11			
	2 years or older	21	7	3.871	1	$<.05$
2)	2 years	13	7			
	3 years or older	8	0	2.100	1	$>.10$

TABLE 5. Effect on homing success of displacing lizards up or down the canyon.

	UP CANYON		DOWN CANYON				
Sex	Home	Not Home	Home	Not Home	X^2	df	p
Males	8	5	7	4	.011	1	$>.90$
Females	13	4	8	9	3.110	1	$>.05$
Sexes Combined	21	9	15	13	1.660	1	$>.10$

sighted again. Some of these lizards may have been killed by predators or moved out of the study area.

Once lizards returned home they remained in the same area, even in subsequent years. Thirty-eight of the 39 successful homing lizards that were captured in the years following their displacement were living in the same home range they had maintained prior to displacement. The 39th animal, a female which had been one year of age when displaced, was located the next year approximately 50 m down the canyon from her previous home range.

Non-returnees were also observed after displacement. Seventeen of 18 such lizards captured in years following their displacement were living in the area of their release. A male which had been one year of age when displaced was recaptured the next year 50 m from the release site in a direction down the canyon and towards its old home area.

B. Parietal Eye and Homing

1. Displacement Studies

a. Control animal data - Home ranges of 60 control animals were measured and converted to 95 percent recapture radii. The mean values for each treatment group are illustrated in Figure 4. A two-way analysis of variance showed no significant differences either between the sexes or among the three treatment groups (Table 6). There was a significant interaction between the parietal eye treatment and lizard sex. S-N-K tests were performed on the male and female data separately to determine if this significant interaction was due to the parietal eye treatment. The tests showed no significant effect of parietal eye treatment in either sex ($p > .05$).

The survivorship of control animals from each of the three

Figure 4. 95 percent home range radii for the three parietal eye treatment groups. Sample sizes appear above histogram bars.

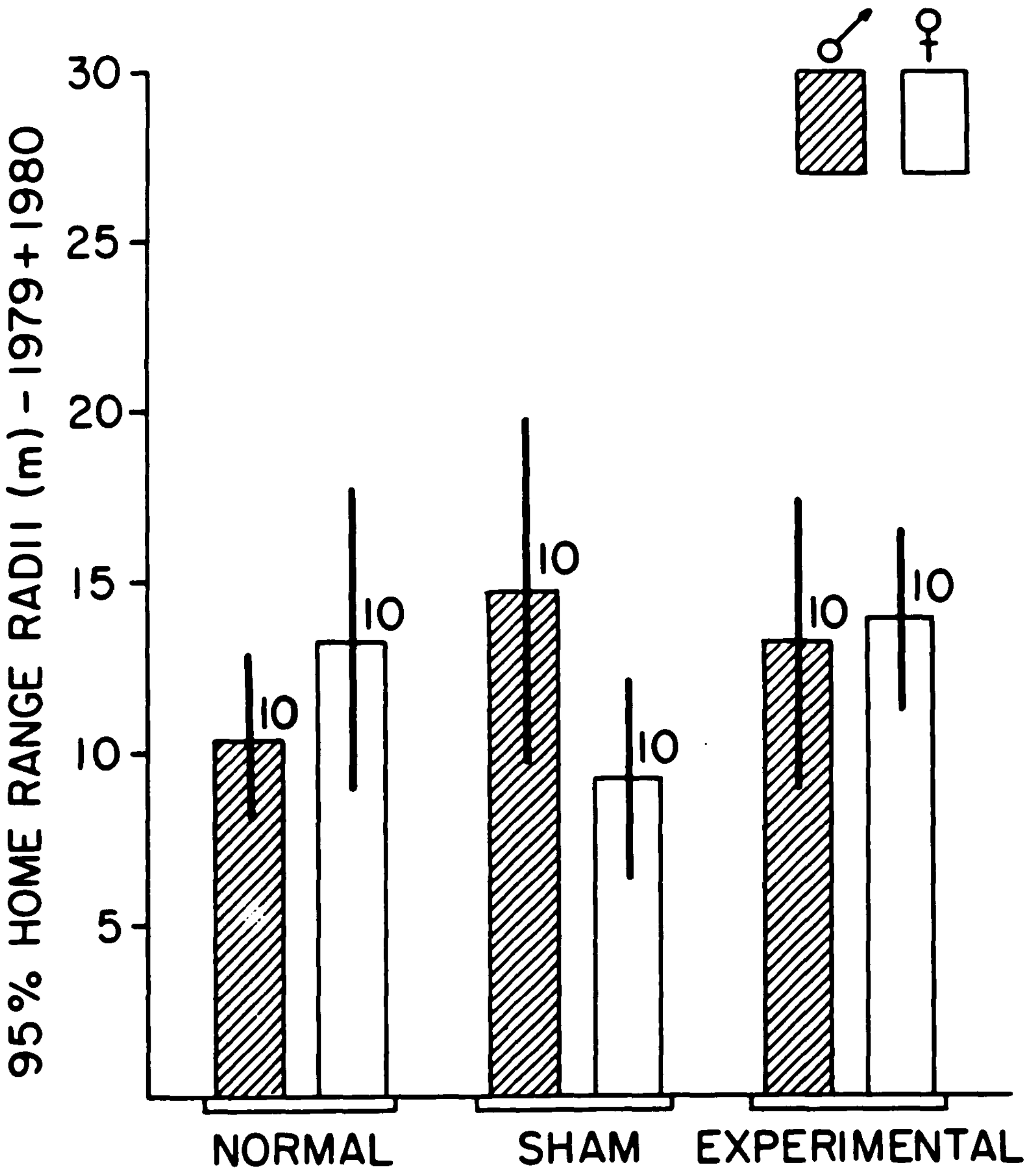

95% HOME RANGE RADII (m) - 1979+1980
30
25
20
15
10
5
♂
♀
10
10
10
10
10
10
NORMAL
SHAM
EXPERIMENTAL

TABLE 6. Two-way ANOVA on recapture radii for lizards in three parietal eye treatment groups.

Source	df	Mean Square	F	p
Parietal Eye Treatment	2	18.06	0.244	$> .75$
Sex	1	6.54	0.674	$> .25$
Parietal Eye X Sex	2	93.70	3.497	$< .05$
Error	54	26.79		

treatment groups is given in Table 7. There were no significant differences in either short-term or long-term survivorship among the three treatment groups for either sex.

The mean number of days lizards were sighted per week for the two years (1979, 1980) is shown in Table 8. Within each year non-parametric Kruskal-Wallis tests showed no significant differences among the three treatment groups for either sex.

b. Homing Data - A comparison of the homing results among the three treatment groups indicates that the parietal eye is important in *S. jarrovi* homing behavior (Figure 5). Contingency table analysis indicated no significant difference between the normal and sham groups for both male and female lizards (Table 9). There was a significant difference, however, between sham and experimental lizards in both sexes (Table 9).

Analysis of the homing successes of lizards displaced more than once also indicates a role of the parietal eye in lizard homing. A total of 17 lizards were initially displaced as normal or sham lizards and then displaced for a second time in a subsequent year. When the condition of lizards during the second displacement was either as normal or sham animals no significant difference in homing success was found between the first displacement and the second one (Table 10). There was, however, a significant decrease in homing success when lizards were displaced for the second time as experimental animals (Table 10). None of these experimental animals successfully homed even though all eight had previously been successful homers.

The times recorded for individual lizards in each of the three parietal eye treatment groups to return home were similar. The mean

TABLE 7. Survivorship of control animals returned to their home ranges. A) Short-term survivorship. Survivors were animals sighted seven days or later after initial treatment. B) Long-term survivorship. Survivors were animals sighted in any subsequent year. S = survivors; NS = non-survivors.

		NORMAL		SHAM		EXPERIMENTAL				
Analysis	Sex	S	NS	S	NS	S	NS	X^2	df	p
A)	Males	8	1	12	5	16	1	3.676	2	>.10
	Females	11	0	13	3	17	2	2.369	2	>.10
B)	Males	2	7	6	11	9	8	2.534	2	>.10
	Females	7	4	8	8	9	10	0.785	2	>.10

TABLE 8. Mean number of days that lizards were active per week for the three treatment groups during the two years of the study (1979, 1980).

Year	Sex	Normal	Sham	Experimental	Kruskal-Wallis Statistic (H)	df	p
1979	Males	3.0	3.2	2.7	0.520	2	.771
	Females	2.6	4.4	3.2	4.978	2	.083
1980	Males	2.0	2.1	2.1	0.297	2	.862
	Females	2.2	2.4	2.1	0.910	2	.635

Figure 5. Percent return success for displaced lizards in the three parietal eye treatment groups. Sample sizes appear on top of the histogram bars.

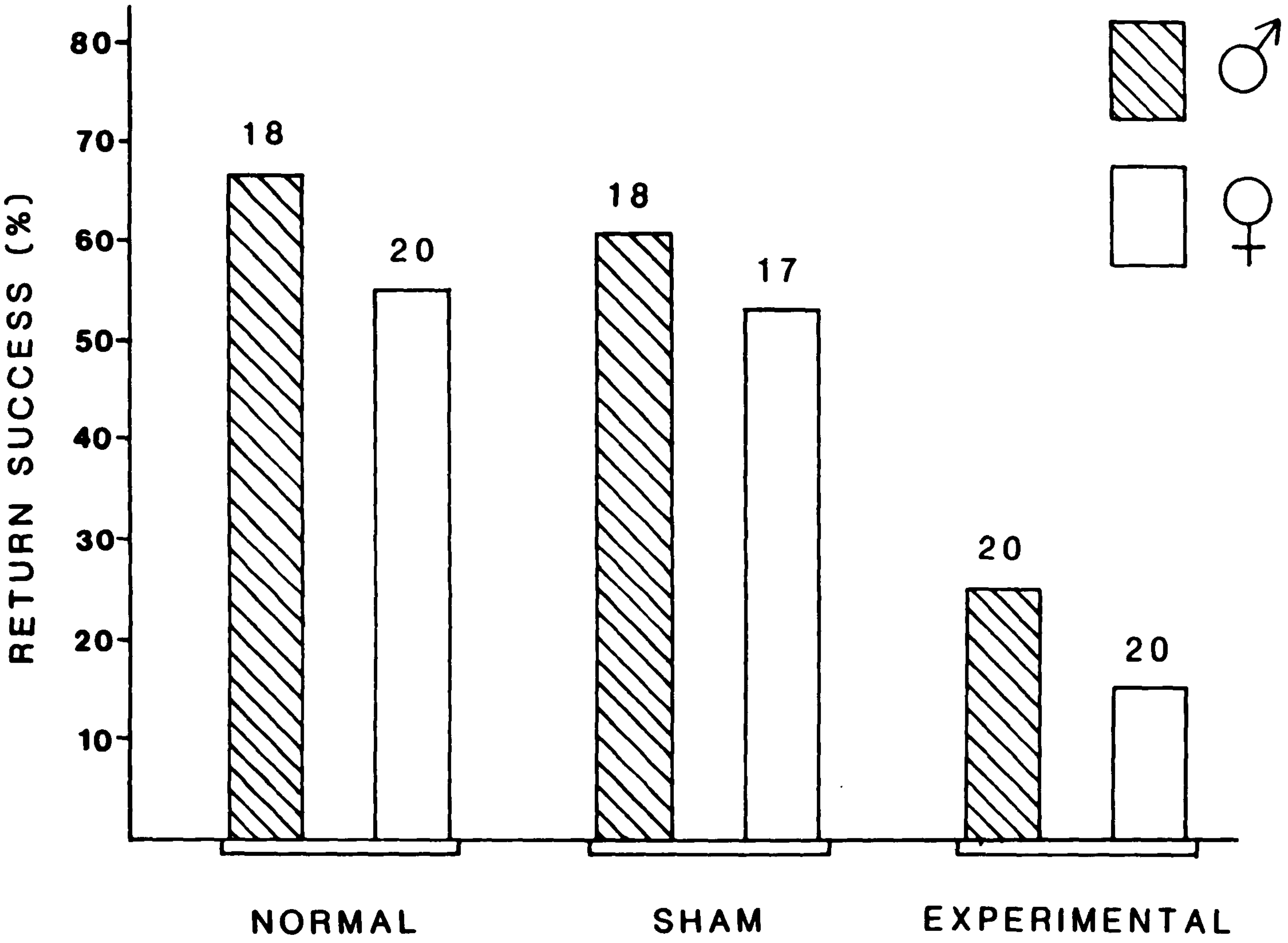

80
70
60
50
40
30
20
10
RETURN SUCCESS (%)
18
20
18
17
20
20
NORMAL
SHAM
EXPERIMENTAL
♂
♀

TABLE 9. Contingency table analysis of effect of parietal eye treatment on homing success.

Sex	Comparison	Treatment	Home	Not Home	X^2	df	p
Males	1)	Normal	12	6			
		Sham	11	7	0.120	1	$>.50$
	2)	Experimental	5	15			
		Sham	11	7	5.068	1	$<.025$
Females	1)	Normal	11	9			
		Sham	9	8	0.016	1	$>.90$
	2)	Experimental	3	17			
		Sham	9	8	6.036	1	$<.025$

TABLE 10. Effect of parietal eye treatment on repeated displacements. In this analysis all lizards were either normal or sham animals during the first displacement.

Treatment During Second Displacement	FIRST DISPLACEMENT Home	FIRST DISPLACEMENT Not Home	SECOND DISPLACEMENT Home	SECOND DISPLACEMENT Not Home	X^2	df	p
Normal or Sham	8	1	9	0	1.059	1	$>.10$
Experimental	8	0	0	8	12.250	1	$<.005$

times, combining male and female data, were: 1) 7.88 days for normal lizards (S.E. = 1.43, N = 16), 2) 7.65 days for sham-treated lizards (S.E. = 1.64, N = 17), and 3) 7.25 days for experimental lizards (S.E. = 2.31, N = 8).

The age-structure of the displaced lizards is presented in Table 11. Chi-square tests showed no significant difference in the number of one-year old versus older lizards among the three parietal eye treatment groups.

Survivorship of displaced lizards was examined (Table 12). No significant differences were found in either short-term or long-term survivorship among the three treatment groups for either male or female lizards (Table 11).

2. Radio-tracking Studies - Analysis of the return pathways of individual lizards from the three treatment groups indicated an effect of the parietal eye treatment on homing orientation. The results of the Hodges-Anje tests on the pathways of 42 lizards are presented in Table 13. The null hypothesis of the Hodges-Anje test, whether the directions traveled by a lizard are uniformly distributed, was rejected for all 14 normal animals of both sexes. This implies that the pathways of homing lizards were oriented. Each of these animals successfully returned to its home range by the day after its displacement. In no case did a homing lizard travel past its home range. The pathway of a normal homing lizard, as well as the Hodges-Anje test of the directions traveled, is shown in Figure 6.

Twelve of 14 sham-treated lizards traveled in significantly non-random pathways (Table 13) and all returned home within two days after displacement. A typical pathway is presented in Figure 7. For two

TABLE 11. The number of displaced lizards in two age groups in each of the three parietal eye treatment groups.

Sex	Age (Years)	Normal	Sham	Exp	X^2	df	p
Male	One	10	10	10			
	Two and older	8	8	10	0.160	2	$>.90$
Female	One	7	9	10			
	Two and older	13	8	10	1.431	2	$>.10$
Sexes Combined	One	17	19	20			
	Two and older	21	16	20	0.669	2	$>.50$

TABLE 12. Survivorship of displaced lizards from the three parietal eye treatment groups. A) Short-term survivorship. Survivors were animals sighted seven days or later after initial treatment. B) Long-term survivorship. Survivors were animals sighted in any subsequent year. S = survivors; NS = non-survivors.

		NORMAL		SHAM		EXPERIMENTAL				
Analysis	Sex	S	NS	S	NS	S	NS	X^2	df	p
A)	Males	14	4	14	4	14	6	1.575	2	$>.10$
	Females	15	5	10	7	9	11	3.746	2	$>.10$
B)	Males	6	12	2	16	6	14	2.785	2	$>.10$
	Females	7	13	8	9	4	16	3.066	2	$>.10$

TABLE 13. Orientation of the return pathways of individual lizards in the three parietal eye treatment groups.

	Treatment	Lizard Number	Number of Sightings	Hodges-Anje statistic (k)	p
A. Males	CONTROL	5324	13	1	.035
		3514	17	0	<.004
		0325	12	0	.006
		629	21	0	<.003
		3333	18	0	<.002
		5122	17	0	<.004
		2324	21	0	<.003
		3105	13	0	.003
	SHAM	4212	12	1	.059
		0422	18	3	.075
		3231	17	0	<.004
		3225	18	0	<.002
		2302	20	0	<.006
		703	21	0	<.003
		3202	18	0	<.002
		0253	18	0	<.002
	EXPERIMENTAL	5111	24	8	>.413
		1434	26	8	.466
		3215	26	10	>.466
		3133	26	7	.235
		344,53	26	9	>.466
		3143	26	11	>.466
		52,411	26	9	>.466
		1313	26	8	.466
B. Females	CONTROL	309	11	0	.011
		2515	24	0	<.004
		113,41	13	0	.003
		5315	17	0	<.004
		0311	12	0	.006
		0322	21	0	<.003
	SHAM	3512	19	0	<.001
		0254	13	0	.003
		3024	19	0	<.001
		0055	17	0	<.004
		2544	19	0	<.001
		3221	16	0	<.007
	EXPERIMENTAL	0313	23	8	>.265
		912	26	9	>.466
		3553	25	9	>.315
		5345	26	8	.466
		0042	25	7	>.315
		1132	23	6	.265

Figure 6. Return pathway of lizard #629, a normal male as shown by the series of connected dots. The circle diagram plots the azimuths between successive sightings as used in the Hodges-Anje test. The line is drawn to minimize the number of sightings on one side of the circle. The Hodges-Anje test statistic (k) is highly significant; in this case ($p < .003$).

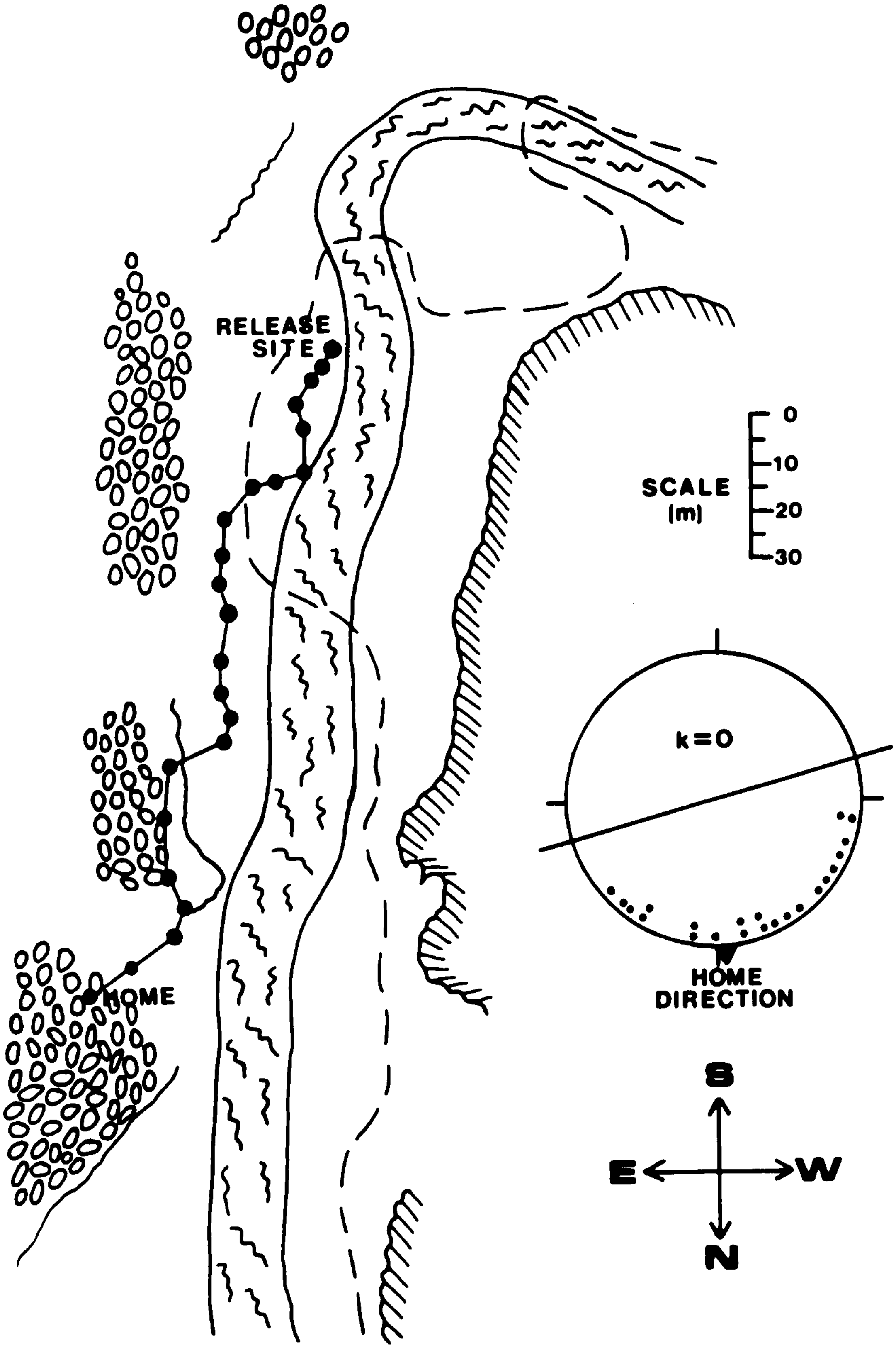
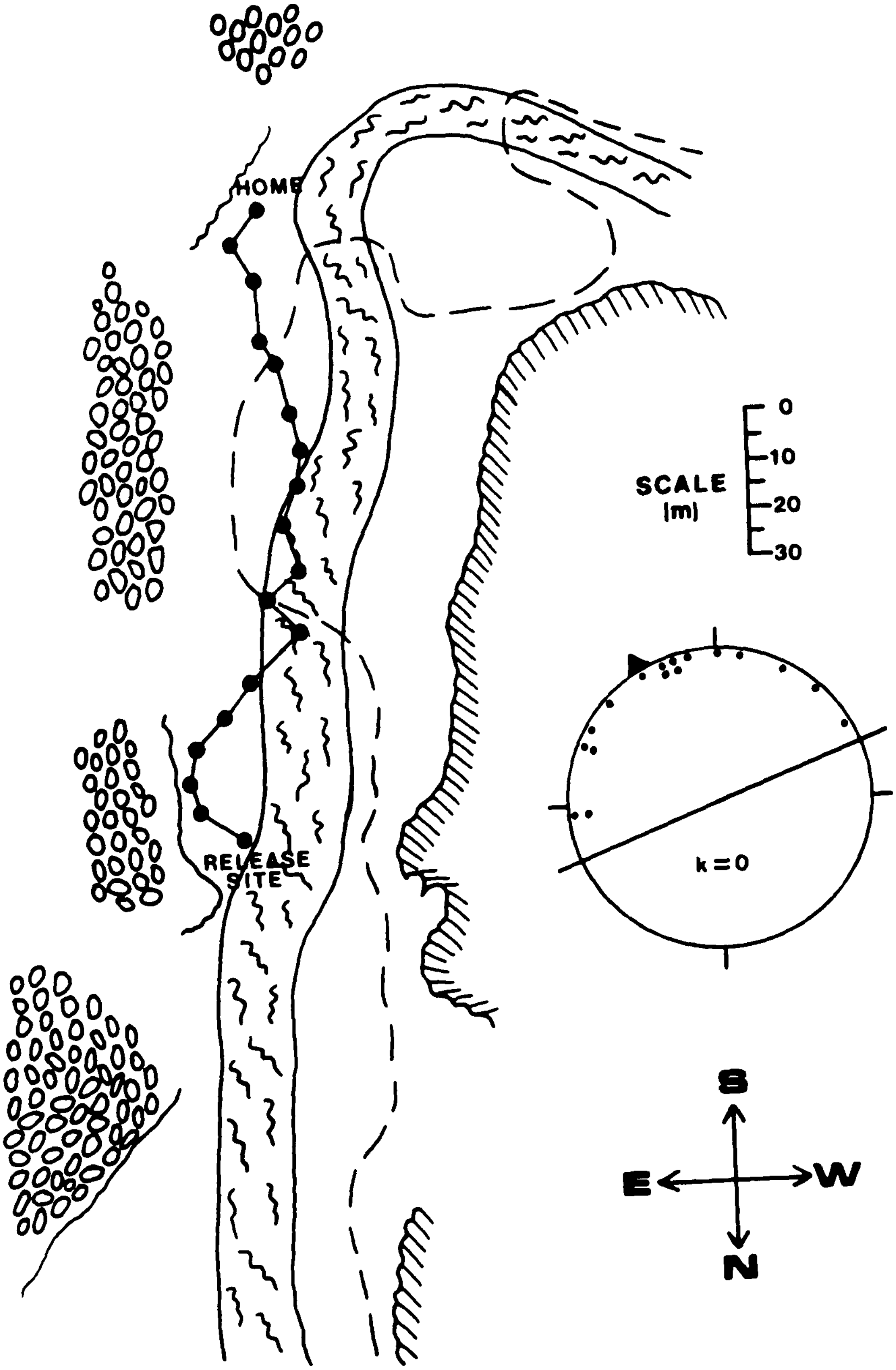

RELEASE SITE
HOME
SCALE (m)
0
10
20
30
k=0
HOME DIRECTION
S
E
W
N

Figure 7. Return pathway of lizard #0055, a sham-treated female. Explanation of diagram is the same as Figure 6. The Hodges-Anje test statistic (k) is highly significant in this case ($p < .004$).


HOME
RELEASE SITE
SCALE (m)
0
10
20
30
k = 0
S
E
W
N

male lizards the pathways were also fairly straight although the Hodges-Anje tests were not significant at the five percent level (Table 13). Both of these lizards initially moved in incorrect directions seemingly heading for the canyon walls (Figures 8 and 9). As soon as they reached a higher vantage point up the walls they headed towards their home ranges.

All fourteen experimental lizards traveled in random directions following displacement (Table 13) and none returned home during the two days of radio-tracking. These animals traveled almost continuously during the daily activity periods and extensively wandered throughout the area surrounding the release site. The movements of an experimental animal are shown in Figure 10.

Results of the Hotelling One-sample T^2 test indicated that as a group the pathways of the normal male lizards were oriented towards home (Figure 11). This is shown by the fact that the 99 percent confidence ellipse does not cover the origin of the unit circle. The pathways of the groups of normal females, sham males and sham females were also significantly oriented in homeward directions. In the experimental lizards, however, the pathways were not significantly oriented towards home. The confidence ellipses cover the origin in both the male and female groups.

The initial orientation of lizards 30 minutes after release is presented in Figure 12. Both male and female normal lizards were significantly oriented towards home as indicated by V tests (Table 14). Of the sham-treated lizards the females were significantly oriented towards home while the male data were not significant at the five percent level as indicated by Rayleigh tests for orientation in

Figure 8. Return pathway of lizard #0422, sham-treated male. The Hodges-Anje test statistic (k) is not significant at the .05 level; in this case ($p = .075$).

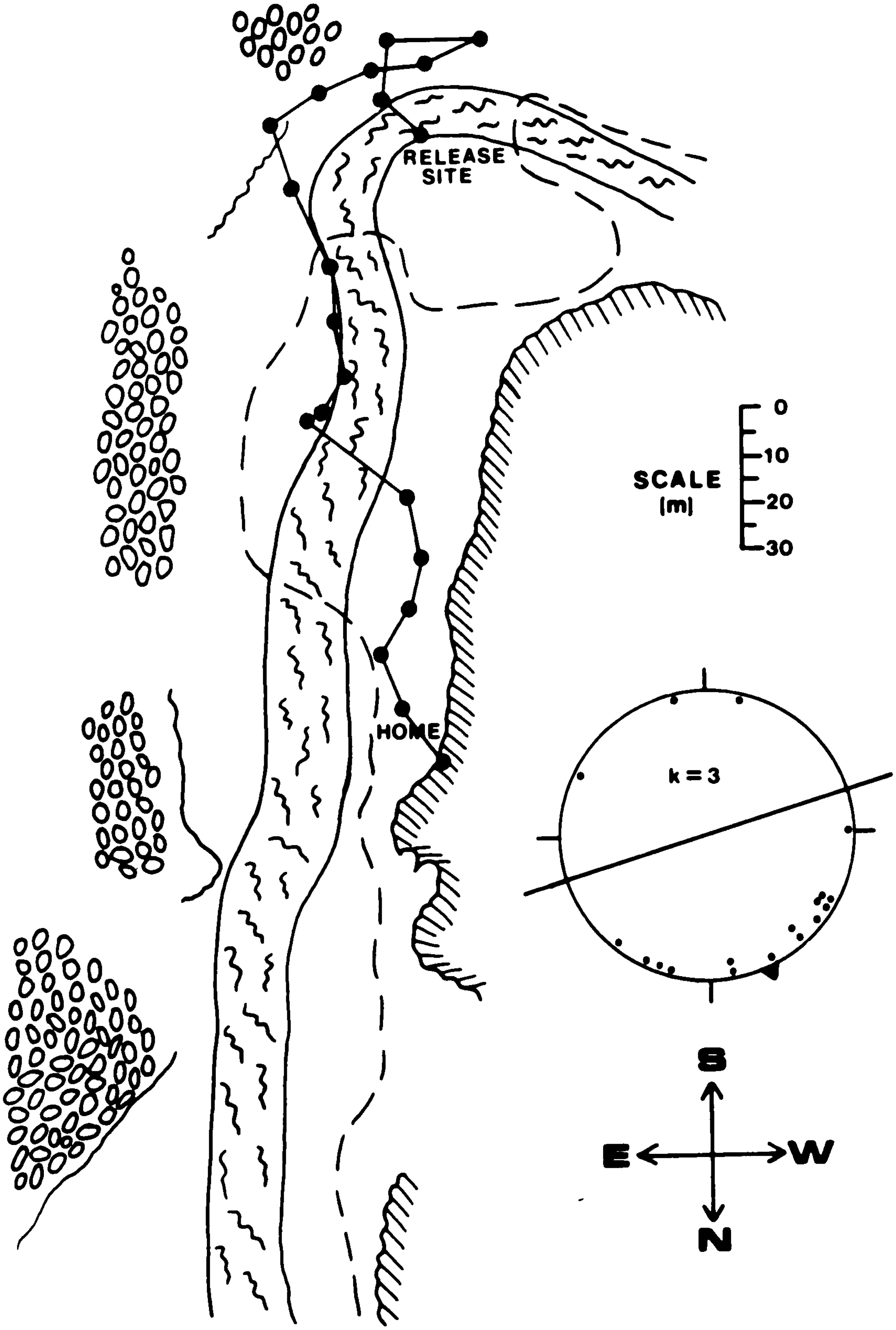

RELEASE SITE
HOME
SCALE (m)
0
10
20
30
k = 3
S
E
W
N

Figure 9. Return pathway of lizard #4212, a sham-treated male. The Hodges-Anje test statistic (k) is not significant at the .05 level; in this case ($p = .059$).

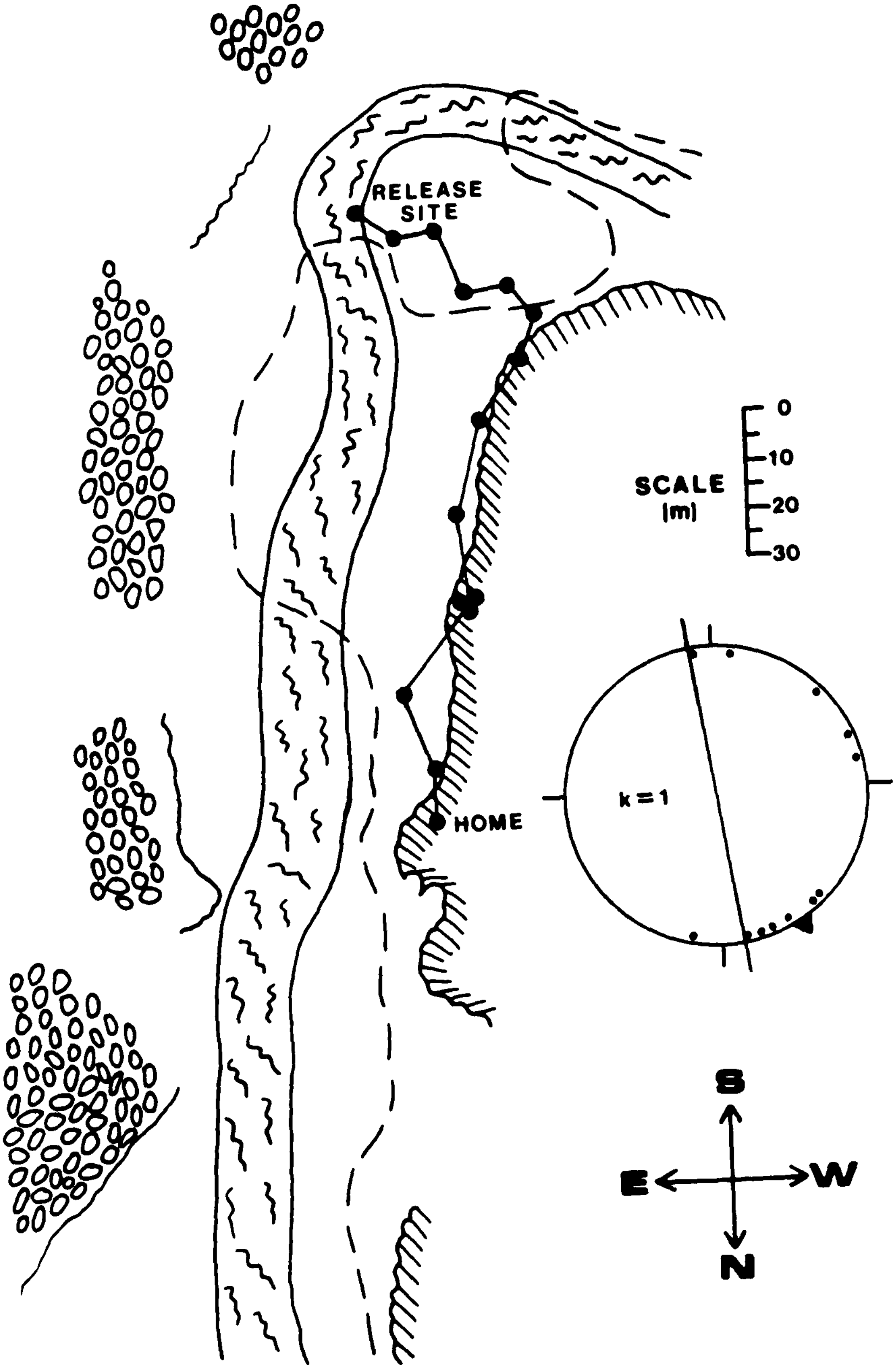

RELEASE SITE
HOME
SCALE (m)
0
10
20
30
k = 1
S
E
W
N

Figure 10. Return pathway of lizard #3143, an experimental lizard. The Hodges-Anje test statistic (k) is non-significant; in this case ($p > .466$).

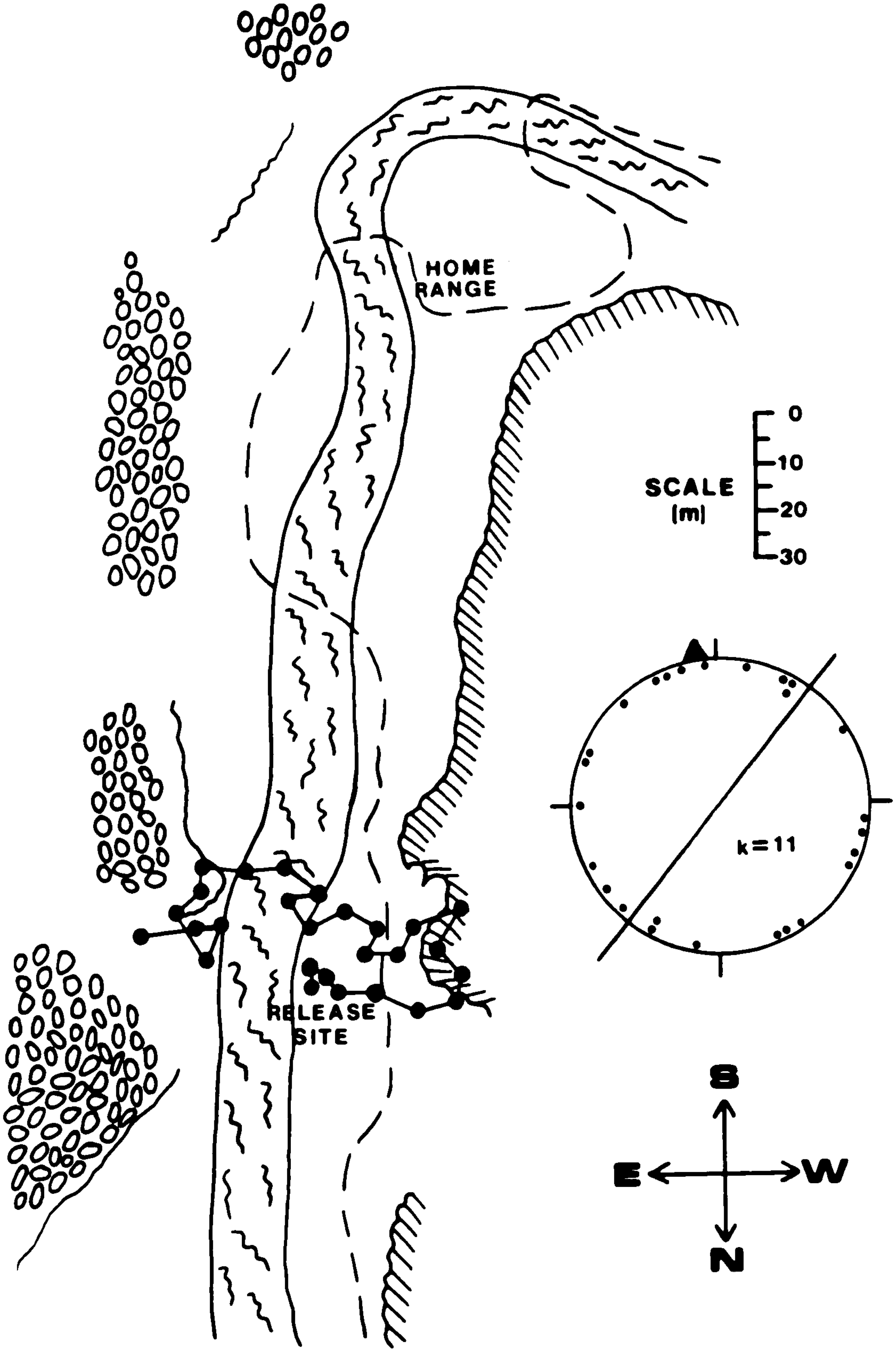

HOME
RANGE
SCALE
(m)
0
10
20
30
k=11
RELEASE
SITE
S
E
W
N

Figure 11. Results of Hotelling One-sample T^2 test. Each dot represents the mean vector of an individual lizard's return pathway. The ellipse represents the 99 percent confidence interval for the Hotelling T^2 test.

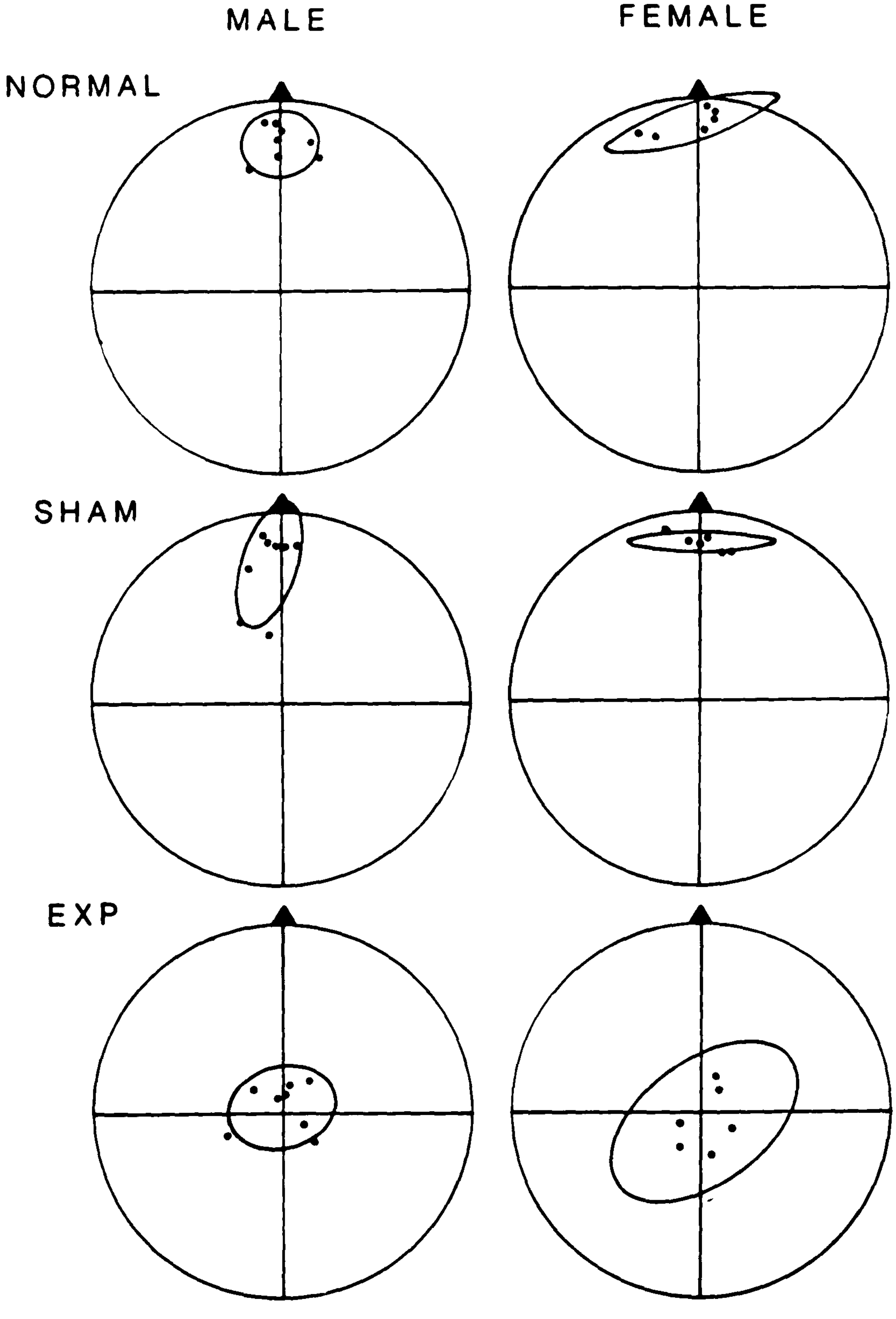

MALE
FEMALE
NORMAL
SHAM
EXP

Figure 12. Initial orientation responses of male and female lizards in the three parietal eye treatment groups. Mean vector shows group direction and, by its length, the amount of dispersion about the mean.

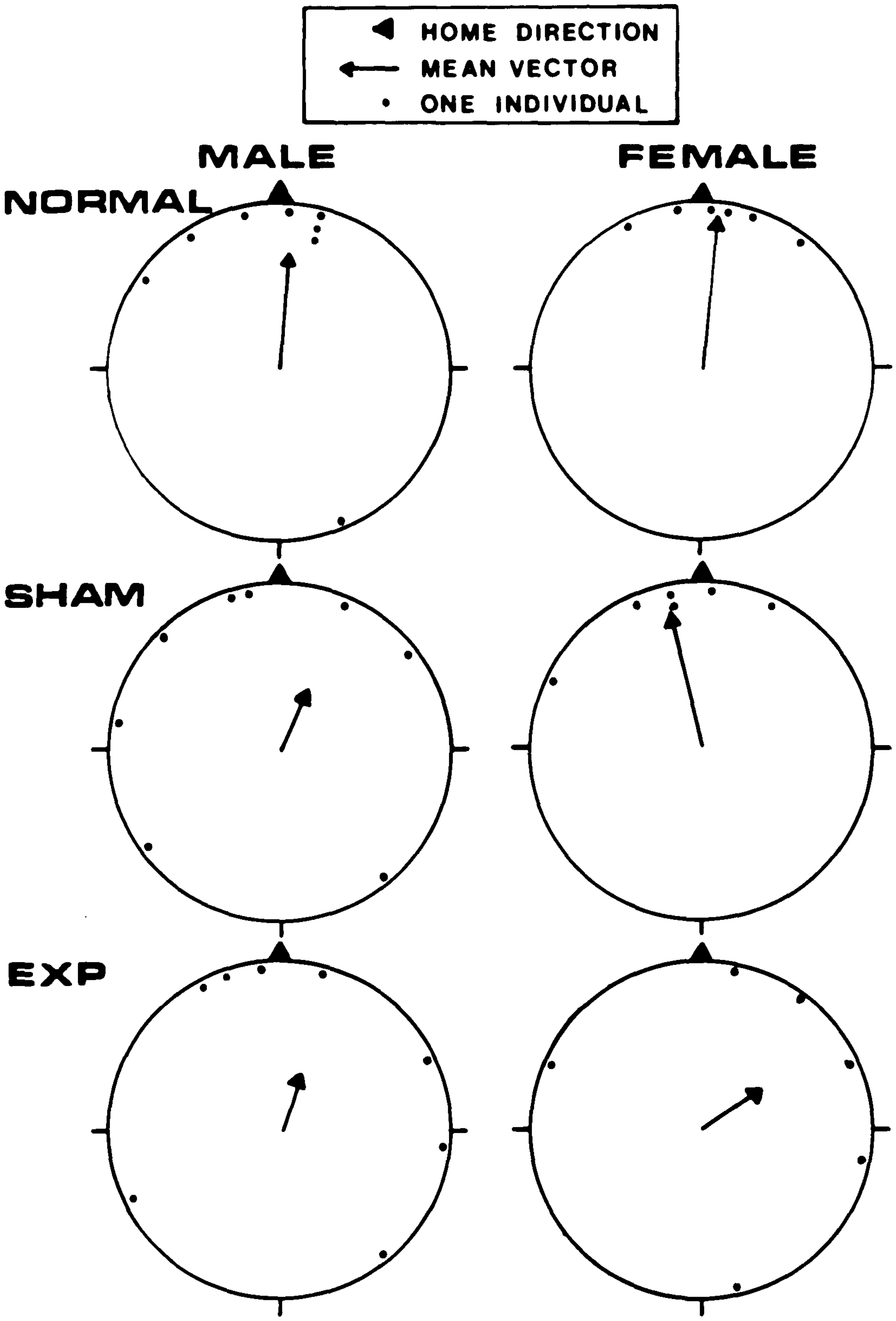

◀ HOME DIRECTION
← MEAN VECTOR
• ONE INDIVIDUAL
MALE
FEMALE
NORMAL
SHAM
EXP

TABLE 14. Initial orientation statistics for the three treatment groups of lizards. The Rayleigh test statistic is a measure of significance of orientation in any direction while the V test is a measure of significance of concentration in the homeward direction.

Sex	Treatment Group	N	Mean Vector	Rayleigh Test Statistic (z)	p	V Test Statistic (u)	p
Males	Normal	8	5°	3.55	$<.025$	2.66	$<.005$
	Sham	8	21°	1.31	$>.10$	1.51	$>.05$
	Experimental	8	17°	1.23	$>.10$	1.50	$>.05$
Females	Normal	6	5°	5.32	$<.001$	3.25	$<.0001$
	Sham	6	13°	4.82	$<.01$	3.02	$<.001$
	Experimental	6	52°	1.00	$>.10$	0.88	$>.10$

any direction and by V tests for homeward orientation (Figure 12, Table 14). The compass bearings of sham males three and one-half hours after displacement, however, were significantly oriented towards home (Figure 13) indicating an improvement in their orientation over time. Experimental lizards of both sexes were moving randomly 30 minutes after release as indicated by both Rayleigh and V tests (Figure 12, Table 14). In addition, their orientation three and one-half hours after displacement was still random (Figure 13) indicating no improvement in orientation over time.

Correlation coefficients were calculated between the azimuths of orientation at 30 minutes after release and the azimuths from the release point to the sighting location three and one-half hours after displacement (Table 15). Significant correlations were found for all normal and sham groups while no correlation existed in the experimental groups (Table 15). This indicated that the normal and sham animals were consistent in their orientation while the experimental animals were not.

C. Parietal Eye and Sun-compass Orientation

Normal lizards maintained for one week on a light-dark cycle in phase with nature, showed significant orientation towards home 30 minutes after their release in the field (Figure 14, Table 16). When lizards were subjected to a six-hour phase advance in the light-dark cycle with respect to the environment, their direction of initial field orientation was shifted counter-clockwise (Figure 14). These animals were significantly oriented in the predicted direction of 270° (Table 16). The mean direction of the normal : advanced phase-shift animals (294°) was shown to be significantly different from the mean

Figure 13. Homing orientation three and one-half hours after displacement. Each dot represents the azimuth from an individual lizard's release point to its sighting location three and one-half hours after release. θ is the direction of the mean vector. u is the V test statistic.

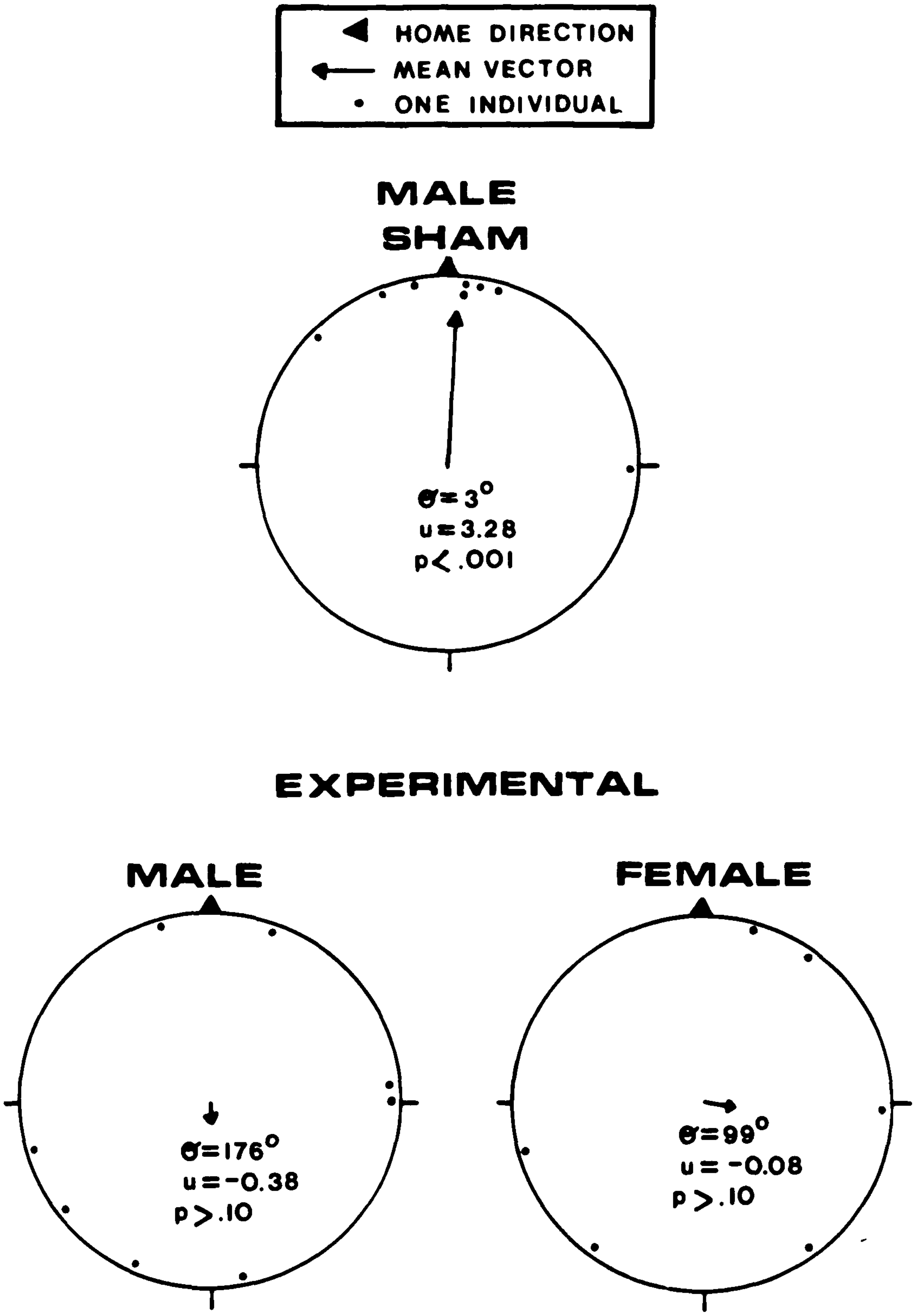

HOME DIRECTION
MEAN VECTOR
ONE INDIVIDUAL
MALE
SHAM
θ=3°
u=3.28
p<.001
EXPERIMENTAL
MALE
θ=176°
u=-0.38
p>.10
FEMALE
θ=99°
u=-0.08
p>.10

TABLE 15. Correlation coefficients calculated between the initial orientation azimuth at 30 minutes after displacement and the azimuth from the release site to the sighting location at three and one-half hours after displacement.

Sex	Treatment Group	N	r	p
Males	Normal	8	.9435	<.01
	Sham	8	.9648	<.01
	Experimental	8	.2251	>.10
Females	Normal	6	.9931	<.01
	Sham	6	.9845	<.01
	Experimental	6	.7559	>.10

Figure 14. Initial field orientational responses of normal and experimental male lizards after entrainment to two different light-dark cycles. The phase-shifted direction is the expected direction of orientation following the advanced phase-shift.

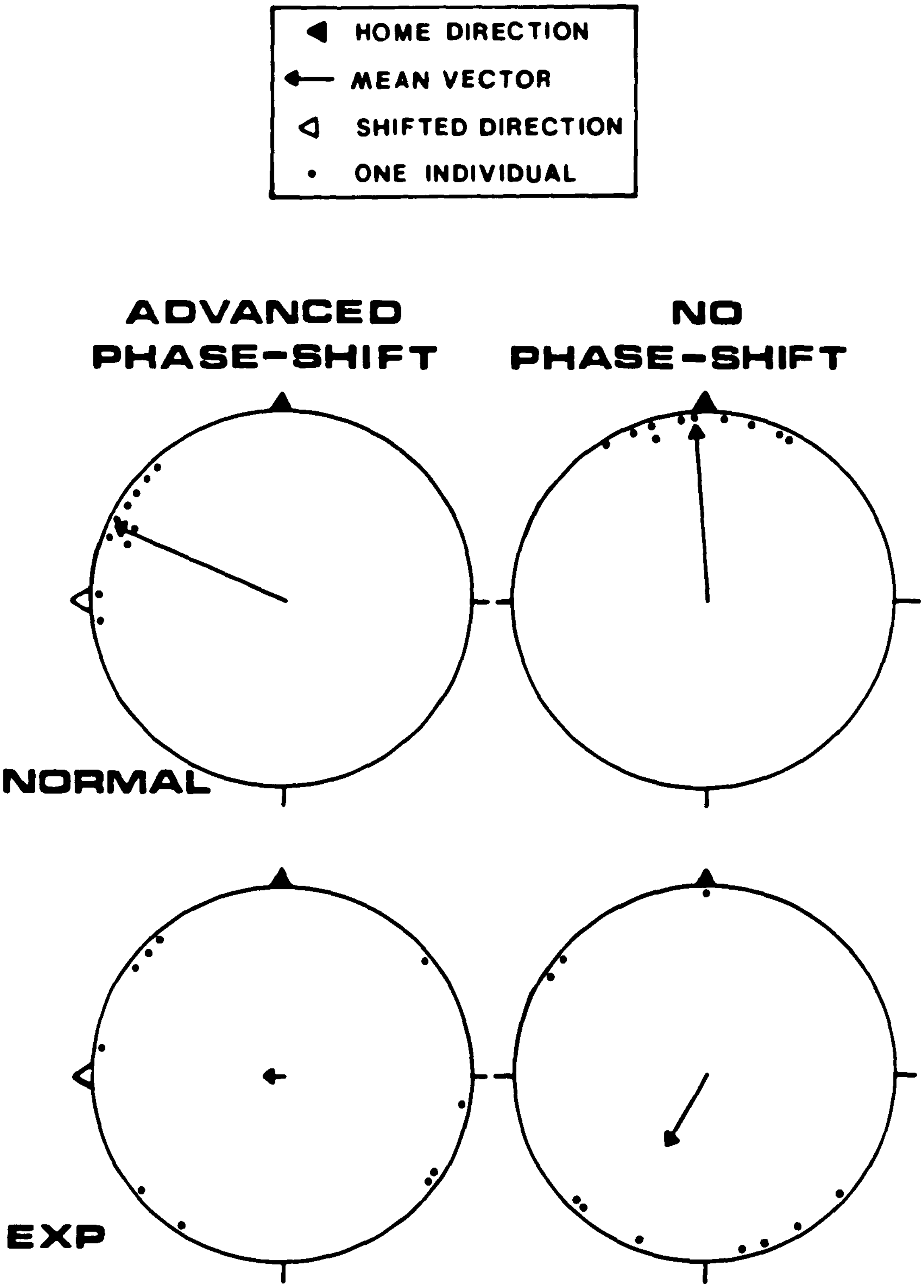

◀ HOME DIRECTION
← MEAN VECTOR
◁ SHIFTED DIRECTION
• ONE INDIVIDUAL
ADVANCED PHASE-SHIFT
NO PHASE-SHIFT
NORMAL
EXP

TABLE 16. Initial field orientation statistics for the four phase-shift groups of male lizards (N : NPS = normal lizards on no phase-shift; N : APS = normal lizards on a six-hour advanced phase-shift; E : NPS = experimental lizards on no phase-shift; E : APS = experimental lizards on advanced phase-shift). The Rayleigh test statistic is a measure of significance of orientation in any direction while the V test is a measure of significance of concentration in the predicted direction.

Treatment Group	N	Vector	Rayleigh Test Statistic (z)	p	V Test Statistic (u)	Predicted Direction	p
N : NPS	10	356°	8.97	$<.001$	4.23	0°	$<.0001$
N : APS	10	294°	9.29	$<.001$	3.92	270°	$<.0001$
E : NPS	10	210°	1.78	$>.10$	- 1.63	0°	$>.10$
E : APS	10	272°	0.12	$>.10$	0.49	270°	$>.10$

direction of the normal : no phase-shift animals (356°) by a Watson's U^2 test ($U^2_{10,10} = 0.39$, $p < .001$). A representative pathway of a normal : phase-advanced lizard following displacement is shown in Figure 15. All of these lizards headed directly towards the canyon walls after release instead of moving in the direction of the no phase-shift lizards, parallel to the length of the canyon.

The two groups of experimental lizards, both the phase-advanced animals and those maintained on a natural cycle, moved in random directions following displacement as indicated by both Rayleigh tests and V tests (Figure 14, Table 16).

D. Parietal Eye and Thermoregulation

The body temperatures of female lizards in all three parietal eye treatment groups were similar for most time periods (Figure 16). The analysis of variance showed no significant differences in mean body temperature among the three parietal eye treatment groups (Table 17). No significant interaction was recorded between the parietal eye treatment and time of day as well as between parietal eye treatment and number of days. In addition, there was no significant effect due either to time of day or the number of days.

The body temperatures of male lizards in the three parietal eye treatment groups were more variable over the times of day (Figure 17). The analysis of variance showed a significant effect of time of day on body temperature but no effect due to number of days since treatment (Table 18). No significant effect was found due to parietal eye treatment although there was a significant interaction between time of day and parietal eye treatment (Table 18). This interaction was further investigated by separate one-way analyses of variance on each

Figure 15. Movements of lizard #703, a normal lizard on a six-hour advanced phase-shift. Explanation of diagram is the same as Figure 6.

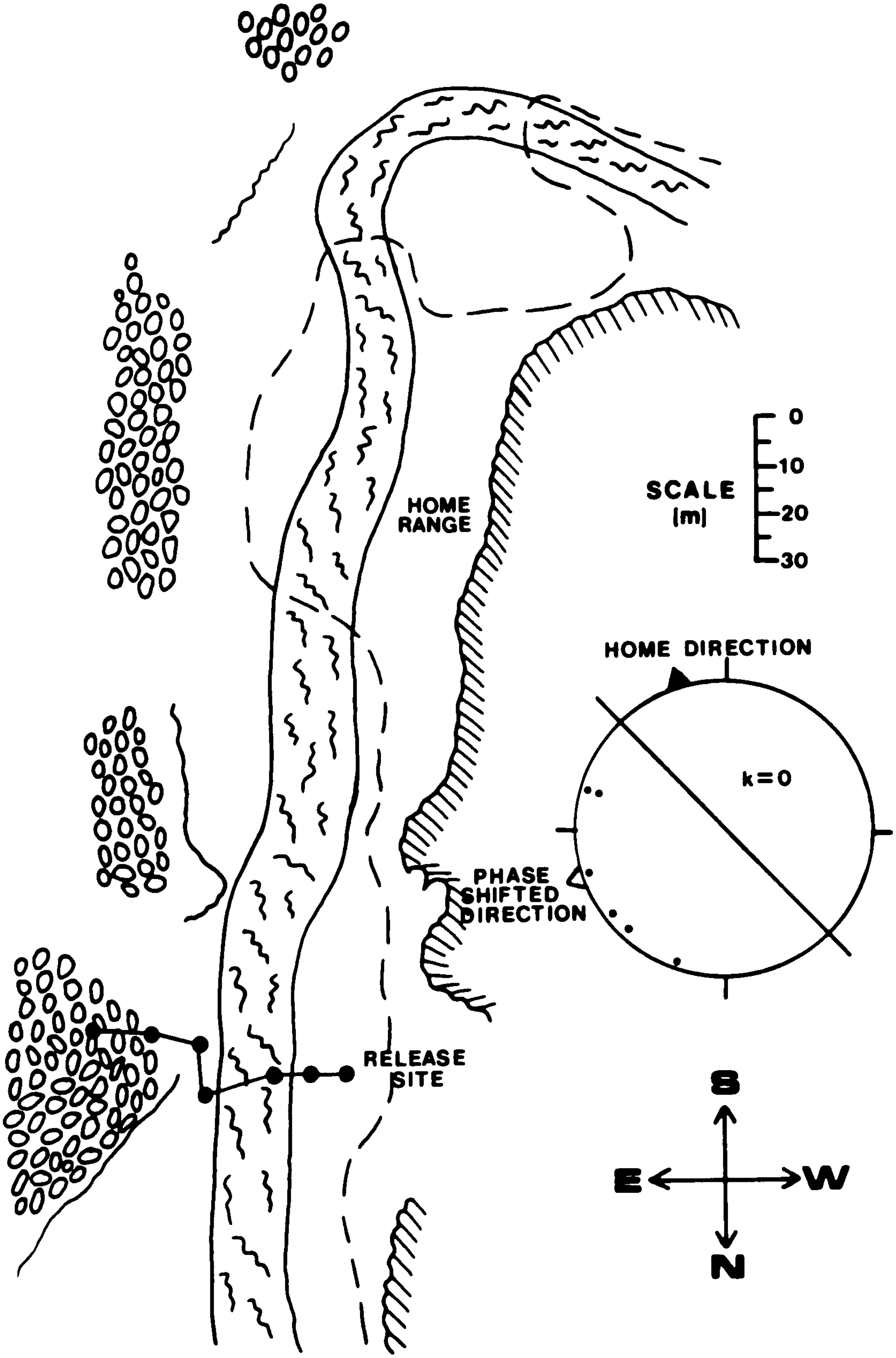
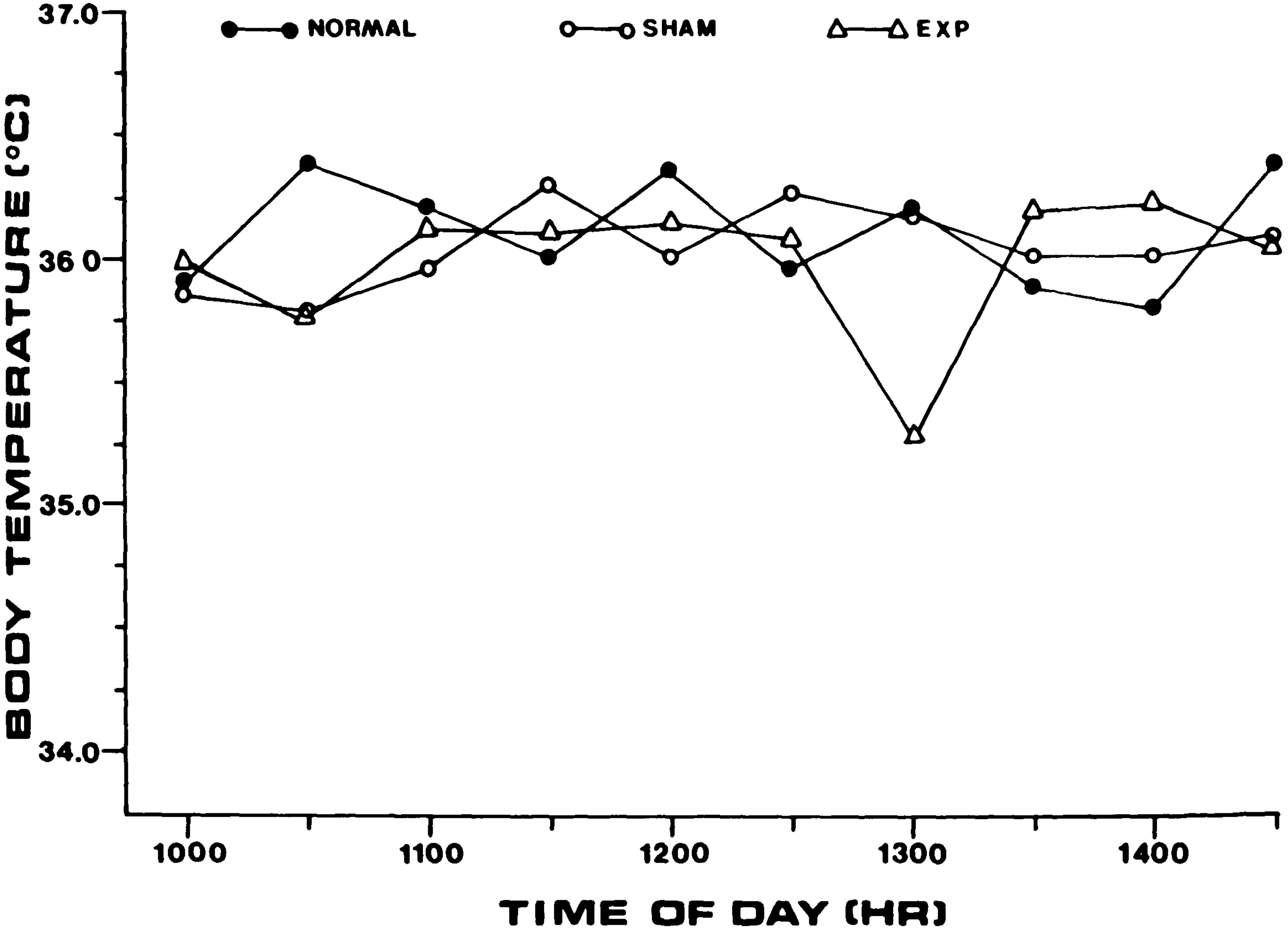

HOME RANGE
SCALE (m)
0
10
20
30
HOME DIRECTION
k=0
PHASE SHIFTED DIRECTION
RELEASE SITE
S
E
W
N

Figure 16. Mean body temperatures of female lizards for the three parietal eye treatment groups. Each data point represents the mean of six individual lizards for two days.



NORMAL
SHAM
EXP
37.0
36.0
35.0
34.0
BODY TEMPERATURE (°C)
1000
1100
1200
1300
1400
TIME OF DAY (HR)

TABLE 17. Female thermoregulation analysis. ANOVA for one grouping factor (effect of parietal eye treatment) and two trial factors (time of day and number of days).

Source	df	Mean Square	F	p
Parietal Eye	2	0.37	0.15	.86
Error	15	2.46		
Day	1	0.23	0.58	.46
Day X Parietal Eye	2	0.14	0.36	.70
Error	15	0.39		
Time of Day	9	0.40	0.50	.87
Time X Parietal Eye	18	0.73	0.92	.56
Error	135	0.80		
Day X Time	9	1.11	1.62	.12
Day X Time X Parietal Eye	18	0.68	0.99	.47
Error	135	0.69		

Figure 17. Mean body temperatures of male lizards in the three parietal eye treatment groups. Each data point represents the mean of eight individual lizards for three days.

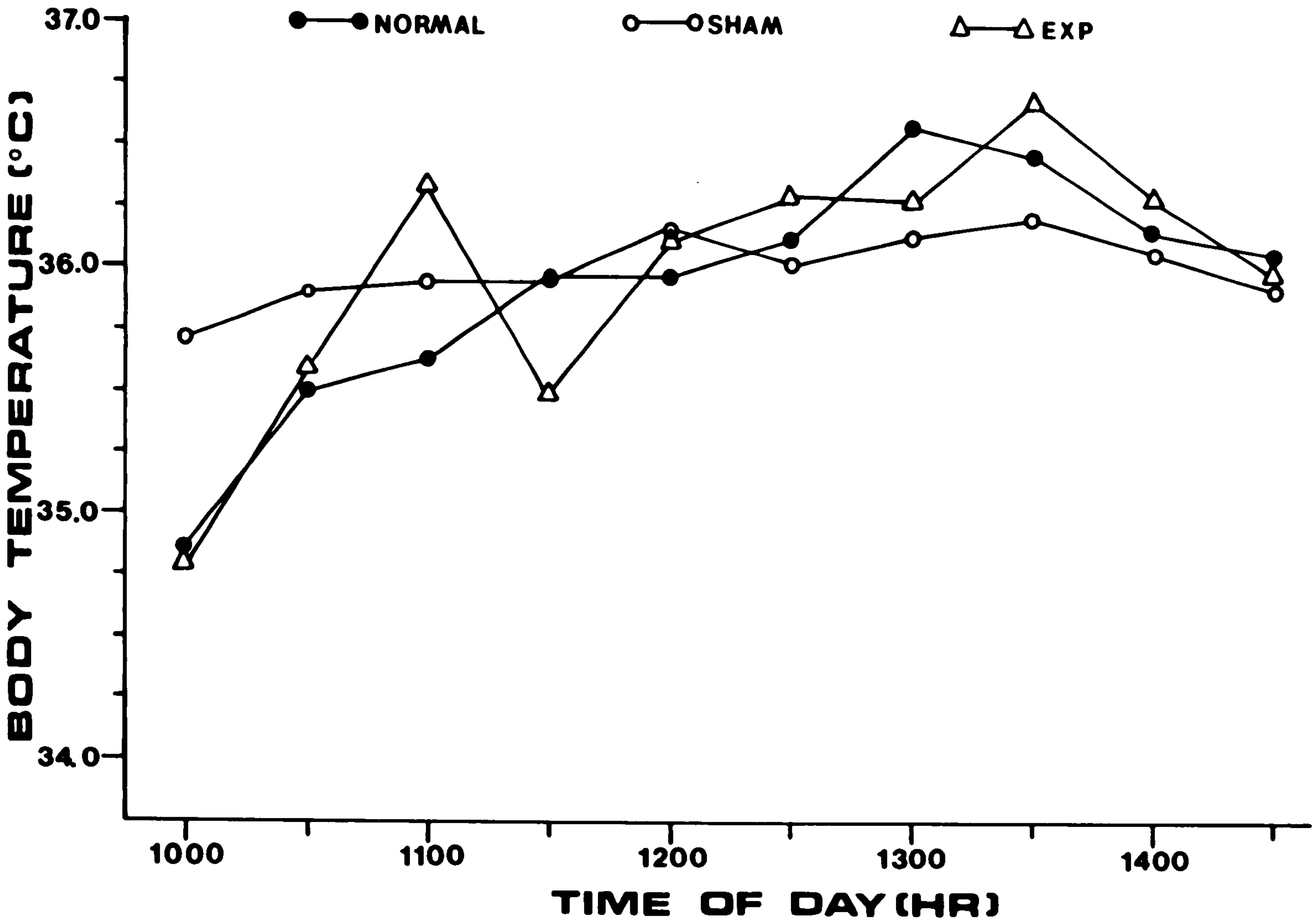

NORMAL
SHAM
EXP
37.0
36.0
35.0
34.0
BODY TEMPERATURE (°C)
1000
1100
1200
1300
1400
TIME OF DAY (HR)

TABLE 18. Male thermoregulation analysis. ANOVA for one grouping factor (effect of parietal eye treatment) and two trial factors (time of day and number of days).

Source	df	Mean Square	F	p
Parietal Eye	2	0.28	0.10	.90
Error	21	2.83		
Day	2	4.20	3.18	.06
Day X Parietal Eye	4	1.01	0.77	.55
Error	42	1.32		
Time	9	9.91	9.40	.001
Time X Parietal Eye	18	1.75	1.66	.05
Error	189	1.05		
Day X Time	18	0.84	0.94	.53
Day X Time X Parietal Eye	36	0.98	1.10	.32
Error	378	0.89		

time period. The only significant effect due to parietal eye treatment was discovered at the hour of 1330 (F = 3.15, df = 2.69, p = .049). S-N-K tests showed this difference to be between the sham-treated and experimental animals.

IV. DISCUSSION

A. Homing Studies on Normal Lizards

Some *S. jarrovi* are capable of returning to their summer home ranges after they have been displaced beyond these home ranges (Figure 3). An animal would be expected to expend the energy to return home when the cost is low or the benefit is high. I believe that in *S. jarrovi* the cost of homing over distances greater than 50 m is relatively high. Such long distance movements are not usually observed in the daily activity patterns of *S. jarrovi*. Ruby (1978) estimated the daily energy expenditures of *S. jarrovi* from the distances animals moved during their daily activity periods. During non-breeding months the mean distance moved by male *S. jarrovi* per day ranged from 12.8 m in June to 28.6 m in August. Mean daily movements by females ranged from 13.7 m in May to 17.0 in August. For a lizard to return home in a few days from distances ranging from 100 to 200 m would require a considerable increase in the distance moved each day. Such increased movement is probably energetically expensive. Huey and Pianka (1981) found that a four- to sixfold increase in the time a reptile is moving may increase its daily energy expenditures by 30 to 50 percent.

Since many *S. jarrovi* are capable of homing despite these energetic costs the benefits must be high. One proposed advantage of homing is the return of an animal to a well-known home range or territory which contains important resources that might be more difficult to obtain in an unfamiliar area. Adult *S. jarrovi* of both sexes are territorial and defend their territories against all size classes (Simon, 1975; Ruby, 1978). Territoriality develops when defense of an area containing critical resources is economical (Brown, 1964; Brown and Orians, 1970). Defendable resources may include mates, display perches or food. Simon (1975) has suggested that during the summer the primary advantage to S. jarrovi of maintaining a territory may be related to food accessibility while in the fall it may be for the facilitation of mating. Ruby (1978) suggested that for male S. jarrovi the advantages of defending a territory are for breeding. In his study, male territory size increased from May until the fall breeding season and shifts of location occurred to incorporate more females in the male territory.

Since S. jarrovi may defend territories to insure an adequate food supply, at least during the summer months (Simon, 1975), homing lizards may simply be returning to an area where they can obtain this critical resource. An animal capable of returning to a known and "private" food source could benefit from more rapid growth than if it remained in an unfamiliar area where it could not immediately establish such a defended resource.

Since this species mates in the fall, the importance of territories for successful breeding could be a factor in the successful homing of adults, especially in males. If a territory is a prerequisite for successful reproduction, the benefit of homing might well exceed its costs. A lizard finding itself in an unfamiliar location in mid-July or August would have to expend large amounts of energy in a relatively short time to successfully establish a new territory before the breeding season. Weintraub (1970) found that non-homing S. orcutti had difficulty establishing new home ranges and territories at their displacement sites.

Homing ability in _S. jarrovi_ varied significantly among the various age groups and seemed to depend upon displacement distance (Figure 3). Juvenile and adult lizards displaced 50 m had homing success rates that were not significantly different (63.6% versus 80%). Only one juvenile _S. jarrovi_ successfully homed from a distance of 100 m and none managed to return from 150 m. The relatively poor homing ability of juvenile _S. jarrovi_ over distances greater than 50 m is consistent with studies on other iguanids. Fitch (1940) displaced predominantly young _S. occidentalis_ individuals and felt that their youth contributed to the negative homing results for this species. An effect of age has also been noted in other studies where the ages of the individual lizards were known or estimated. Young _S. orcutti_ (those in their first year after hatching) had a lower return success than both juvenile (those in the second year after hatching) and adult lizards (Weintraub, 1970). Significantly fewer juvenile than adult _S. graciousus_ returned home after displacement (Guyer, 1978).

The poor homing success of juvenile _S. jarrovi_ can be interpreted in several ways. It may indicate that juveniles: 1) have not yet developed an attachment or familiarity with a specific area to which they could return, 2) they are incapable of returning home from unfamiliar locations, or 3) they do not home for some other reason unconnected with the ability to do so.

An animal that lacked any affinity for a home range would not be expected to return to the exact location it had been displaced from. Instead it would simply remain in the area of its release or wander somewhere else. An animal that had only lived in an area for a short period of time might have a relatively weak attachment to it. This is a possibility for juvenile *S. jarrovi*, since they were born in late spring and had only been residing in the study area for approximately two months prior to displacement. Most juvenile *S. jarrovi* returned home when displaced 50 m, however, which suggests that these young animals had some sort of attachment to the area in which they had lived.

While juvenile *S. jarrovi* consistently returned home when displaced only 50 m, they did not do so from longer distances. This could mean that the cues necessary for homeward orientation were available to juveniles displaced 50 m but were not available to those displaced 100 m or more. Familiar landmarks is one such class of distance dependent orientation cue. In other words, juvenile *S. jarrovi* may be familiar only with areas within 50 m of their home ranges. Ruby (1976) found that juvenile *S. jarrovi* did not show fidelity to specific locations within the area in which they were living for several months. While most juveniles in the South Fork study area establish home ranges within 50 m from the area of their birth (Simon and Middendorf, 1980) some have been noted to move considerable distances within the canyon. Thus, it is likely that many juvenile *S. jarrovi* are familiar with areas within 50 m of their home ranges while only a few would have previous experience at 100 m. In addition, a distance of 50 m is short enough that random wandering would frequently bring a young lizard to a recognizable area from which it could orient towards home.

A juvenile lizard capable of homing might not return home for other reasons. Juvenile lizards are subordinates in the population and cannot defend a territory against adult (Simon, 1975; Simon and

Middendorf, 1980; Ruby, 1976). In being subordinate the strength of the relationship between a juvenile lizard and its home range is probably weaker than that of an adult. Without a significant attachment to a home area the costs to a juvenile of homing from distances greater than 50 m might easily exceed the benefits. When displaced out of their home areas into another suitable area juvenile lizards may set up new home ranges at the release site instead of expending the energy necessary to return home. All nine of the non-homing juvenile _S. jarrovi_ that were repeatedly sighted after displacement were observed to have established home ranges in the area of release. The establishment of new home ranges instead of homing could be reproductively advantageous to these displaced juveniles. _S. jarrovi_ mates in the fall and Ballinger (1973, 1979) found that 41-84 percent of the juvenile females born in the spring are sexually mature five months later. It may be more efficient for a juvenile to remain at the displacement site and divert the energy that otherwise would be expended in returning to the old home area to the rapid growth needed for sexual maturation.

Homing success was also affected by lizard age in _S. jarrovi_ after their first season. One year old lizards had a significantly lower homing success than older lizards at the 150 m displacement distance (Table 4). Weintraub (197) also noted a lower homing success in male, but not female, yearling _S. orcutti_. This lower homing success of yearling _S. jarrovi_ might also be attributable to a weaker attachment to the home range.

The attachment of an adult lizard to its territory may be affected by its age and prior experience. Ruby (1978, 1981) has shown significant differences in the territorial and mating behaviors of one year old S. jarrovi as compared to older lizards. In both males and females larger and older animals tended to "win" more territorial encounters. For male S. jarrovi this sometimes resulted in one year old animals being evicted from the area by the larger males. Those one year old males that remained in the area were generally excluded from the best territories by the larger males. During the breeding season the males known to have mated were significantly larger and older than other males. In addition, male reproductive success (probable number of offspring sired) was significantly correlated with lizard age and snout-vent length. Thus, it appears that the advantages of maintaining a territory in male S. jarrovi are mainly accrued by older individuals. This is not to suggest that one year old males never obtained the higher quality territories. The older, dominant males did not always survive to the breeding season and when a vacant territory appeared younger males could shift their territory position to the more desirable location (Ruby, 1976). In general, however, a one year old male who suddenly finds himself in an unfamiliar area may be no worse off in the new site than in his old home range. It is likely that he will be a subordinate in both locations. The costs of homing might easily outweigh the benefits of returning in such a situation. A male remaining at the displacement area could divert his energy to growth, which might enhance his chances of reproductive success at the new location. Ruby (1976) has suggested that female S. jarrovi may selectively mate with larger members of the one year old age class. On the other hand, one year old males which have maintained higher quality territories or have been dominant might find it to be more advantageous to expend the energy necessary to return home. Thus, homing success in one year old males might be expected to be lower and more variable than in older lizards, with the motivation of a given yearling to home depending on the circumstances of that particular animal.

The lower homing success of one year old females could also be related to their territorial behavior and subordinate positions in the population. Ruby (1976) found that 48 percent of one year old females abandoned their previous home ranges whereas only 16 percent of older females did so. One year old females are subordinate to, and generally avoid, older females. It is likely that older females maintain territories in more desirable locations than one year old females. While this does not exclude young females from breeding it could affect their growth and reproductive potential. Litter size in _S. jarrovi_ increases with female snout-vent length (Ballinger, 1973). While the reasons for maintaining territories in male and female _S. jarrovi_ are probably not identical, one year old lizards of both sexes may be less attached to their areas due to their subordinate positions in the population. This could be a major factor influencing the lower homing success of this age group.

When displaced, older _S. jarrovi_ return home in significantly higher numbers than one year old lizards, with 100 percent homing success of the three year and older age group (Table 4). It is likely that the attachment of a lizard to its home range is greater in these older lizards which have the advantages of size, age and dominance in keeping a high quality territory. In addition, it is probable that these individuals have successfully bred in their territories at least once and possibly three times. Such an animal finding itself in an unfamiliar area would have to spend considerable amounts of energy to establish its dominance in a new area of unknown quality. The advantages of returning home, minus the costs of homing, could easily outweigh the disadvantages of remaining at the displacement site.

The importance of maintaining a constant home range over periods of years is shown in the recapture data of homing lizards. All lizards that successfully homed, with a single exception of a one year old female, which were recaptured in years after their displacement were found living in the same home range they had maintained prior to their displacement. One of these lizards, a female, has lived in the same home range for at least six years, including years before and after her initial displacement in 1978 (Bissinger and Simon, unpublished data).

Homing ability in S. jarrovi did not differ between the sexes (Table 3). This is in contrast to S. orcutti where all age classes of females had a poor return success (Weintraub, 1970). Basic differences in the territorial behavior of these two species might account for the lower homing ability in female S. orcutti. While female S. jarrovi are highly territorial (Simon, 1975; Ruby, 1978) Weintraub (1970) suggested that female S. orcutti might have a weak attachment to a specific home area. A review of the literature on territorial behavior in lizards (Stamps, 1977) indicated that most male iguanids tend to be aggressive and territorial while females of many species are more passive and non-territorial. Such may be the case in S. orcutti females (Mayhew, 1963).

Non-territorial lizards, such as female S. orcutti, may have never developed a good homing ability or simply lack sufficient motivation to consistently return home. The homing data on the non-territorial *Phrynosoma douglassi* also support this view (Guyer, 1978). Only 3 of 31 *P. douglassi* that were displaced returned home. *Phrynosoma* species are a major exception to the general phenomenon of territorial behavior in male iguanid lizards (Carpenter, 1967). Most other reports of homing behavior in lizards, including this study, have concerned iguanid lizards which typically maintain territories. Thus, homing may be a common ability in territorial species while relatively uncommon in non-territorial lizards.

Previous studies of homing behavior in lizards (Weintraub, 1970; Krekorian, 1977; Guyer, 1978) have shown that return success decreased with increasing displacement distance until at some point no lizards were found to return home. While no significant effect of displacement distance was noted in adult *S. jarrovi* there was a trend towards lower success at 200 m (Figure 3). Longer displacements were not attempted so it is not known if there is a distance beyond which *S. jarrovi* cannot home. The relatively good homing success of *S. jarrovi* at distances up to 150 m, as well as the decrease at the greater distance, is consistent with all previous studies of lizard homing (Weintraub, 1970; Krekorian, 1977; Guyer, 1978). The maximum homing distance for all species studied is less than 300 m.

Studies on other taxonomic groups of vertebrates have also shown a distance effect. Lower homing success with increasing distance occurs in small mammals (Stickel, 1949; Murie, 1963; Robinson and Falls, 1965; Bovet, 1972; Furrer, 1973; Cooke and Terman, 1977; Parsons and Terman, 1978), salamanders (Twitty, Grant and Anderson, 1967;

Kleeberger and Werner, 1982) and turtles (Gould, 1957, 1959; Emlen, 1969; Ernst, 1970; Lemkau, 1970; Carroll and Ehrenfeld, 1978; Barzilay, 1980).

A possible implication of this inverse relationship of homing success and displacement distance is that displaced animals are simply piloting their way home. Griffin (1952) defined three types of orientation responses. Type I (piloting) is goal-oriented movement using familiar landmarks. Type II (compass orientation) is the ability to orient in a fixed compass direction without reference to landmarks. In Type III orientation (true navigation) the animal is able to select the direction toward a goal such as home when released in unfamiliar territory. The use of these three terms does not imply the use of any particular mechanism. Several quite different models can be proposed for each type of orientation ability. One suggested Type I mechanism is termed "intermediate-range homing" by Carroll and Ehrenfeld (1978). In such a situation animals are released outside their familiar area, but close enough that some sensory cues emanating from or linked to their home environment (e.g., olfactory cues, visual landmarks) may still be available (Able, 1980). It is generally assumed that if the cues were not linked to the home area the animals would be equally able to return home from displacement sites far from their home ranges.

Olfactory mechanisms have been suggested for a variety of homing amphibians (Twitty, 1959; Twitty, Grant and Anderson, 1968; Grant, Anderson and Twitty, 1968; Madison, 1969, 1972; Barthalmus and Bellis, 1972) and turtles (Barzilay, 1980). Such cues were not investigated in this study of S. jarrovi homing and thus cannot be ruled out as possible homing cues.

The use of visual landmarks has been suggested to explain the homing ability of S. orcutti (Weintraub, 1970). These lizards were found to home better from release points in which their home areas were visible. It seems unlikely that the success of homing in S. jarrovi, however, can be attributed to the lizards being able to visually recognize their home areas from afar. The forested canyon in which this study was performed would effectively block such long distance vision. At short distances (50 m) the lizard may have been able to see its home range by climbing a tree or large boulder, but this would not be very effective at longer distances.

Another interpretation of the marked decline in homing success at greater distances found in many species is that some animals had been displaced to areas outside their area of familiarity. The generally accepted view concerning small mammals is that homing is achieved by a combination of random wandering from long distances and movement through familiar terrain within a "life range" which is considerably larger than the normal home range (Furrer, 1973). Familiarity with a larger area is said to be accomplished by occasional excursions outside the home range. The possibility exists that such an explanation could account for the homing success of some S. jarrovi. Each year there is a fairly large immigration of juvenile lizards into this study area (Simon and Middendorf, 1980; Bissinger and Simon, unpublished data). The home ranges of juvenile S. jarrovi tend to be less stable than those of adults (Ruby, 1978; Bissinger and Simon, unpublished data). Some juveniles in the South Fork population have been noted to move their home ranges distances up to 140 m within the period of only a few weeks, while others move very little. In addition, the home ranges of some one year old lizards have been relocated up to 200 m from the areas in which they were last recorded during the previous year (Bissinger, unpublished data). It is not known whether these individuals moved when they were juveniles or early in the following year. Any lizard which had made such a move as either a juvenile or a one year old, however, could have a knowledge of the terrain outside of its normal home range which might possibly help in any homing trial.

Such an explanation cannot account for the homing success of all members of the population, however. Simon and Middendorf (1980) found that most juveniles in my study area do not disperse far from the area of their birth. Of the juveniles that survive until the next summer the majority are relocated in the same home range (Bissinger, unpublished data). Long-term records on this population indicate that most lizards occupy the same summer home ranges year after year. I cannot discount the possibility that individual _S_. _jarrovi_ might occasionally make long-distance excursions to areas outside of their home ranges. There is no evidence of such movements, however, even after six consecutive summers of recording the daily locations of marked lizards (Bissinger and Simon, unpublished data). The lizards that have made long-distances moves have never been observed to return to a previous home range. It thus seems very unlikely that occasional summer excursions, which would familiarize individual lizards with areas 150 m from their home ranges, occur.

This still leaves the possibility that lizards become familiar with other areas of the canyon during the non-summer months. Ruby (1976, 1978) found that male _S_. _jarrovi_ wandered farther during the fall breeding season than at other times of the year. These movements, however, were not long-distance excursions to other areas. Rather they were extensions of stable home ranges which simply were enlarged by 30 to 40 percent. Thus, it is unlikely that this increased activity in the fall would allow a lizard to become familiar with a location greater than 100 m from its summer home range.

The annual migrations of S. jarrovi considerably expand the familiar "life range" of a lizard over its summer home range. Conceivably this could aid the lizards in homing by the use of familiar landmarks. The patterns of movement during these migrations make this unlikely, however. Individual lizards leaving their winter areas moved down the rocky walls to lower elevations in the canyon bottom where their summer home ranges were located. These movements were in a direction perpendicular, not parallel, to the length of the canyon. Since the direction of displacements was parallel to the length of the canyon, it is very unlikely that these migrations considerably increase an individual lizard's familiarity with the canyon bottom, the only area where their homing behavior was examined.

Discovery of a distance effect on homing is frequently used to discount the possibility of a true navigation response. A distance effect has been reported, however, in homing pigeons (Matthews, 1955, 1963; Schmidt-Koenig, 1964; Wallraff, 1967), a species with a well-documented navigational ability. Thus, it does not seem sufficient to base predictions about homing mechanisms solely on displacement distance data.

Another type of homing response which could result in successful homing without the utilization of a true navigation capability is compass orientation (Type II: Griffin, 1952). This type of response has frequently been shown in animals that orient to shorelines: amphibians (reviewed in Ferguson, 1967), turtles (DeRosa and Taylor, 1978, 1982), alligators (Murphy, 1981) and watersnakes (Newcomer, Taylor and Guttman, 1974). For *S. jarrovi*, however, such Type II responses can be eliminated as an explanation for their homing behavior. Lizards were found to successfully home from opposite directions, indicating no stereotyped movement patterns (Table 5).

Type II orientation cannot be entirely ruled out for all *S. jarrovi* movements, however. *S. jarrovi* migrate considerable distances (up to 200 m) to winter aggregation sites (Ruby, 1977; Bissinger, unpublished data). It is possible that a Type II response could be utilized to set a fixed compass direction between the summer home range and the wintering area and vice versa. This possibility has not yet been investigated in *S. jarrovi*.

The time taken by displaced lizards to home is only approximate. Individual *S. jarrovi* are not always active every day or for all of the daylight hours (Simon and Middendorf, 1976). In addition, lizards that are active may be sitting in locations, such as tops of large boulders or high up in trees, that are not visible to the researcher. Thus, it is possible that a lizard may have returned to its home range shortly after displacement but was not sighted for several days.

The homing times recorded in *S. jarrovi*, however, are similar to those reported for *S. orcutti* (Weintraub, 1970), *Dipsosaurus dorsalis* (Krekorian, 1977), and *S. undulatus* (Noble, 1934). Individuals of these three species were usually found at home within 20 days if the study area was frequently monitored. Lizards that failed to home within 20 days usually never homed. In *S. jarrovi* 85 percent of all individuals returned home within 20 days. The seven lizards that were not seen home until later dates all lived near the boundaries of the study site, many near the canyon walls. The probability of not seeing a lizard when it is active is higher in this situation than when the lizard's home range is closer to the center of the study area since portions of the lizard's home range may lie outside those areas regularly searched (Bissinger, unpublished telemetry data). In thus seems likely that these lizards had returned home sooner but were not immediately sighted.

Another homing mechanism that S. jarrovi could use is the orientation to gravitation cues (geotaxis). Lizards displaced up the canyon had to move downhill to return home while lizards displaced down the canyon had to walk uphill. There is little evidence to date for the influence of geotaxis on orientation by reptiles and amphibians. Barthalmus and Bellis (1969) found that significantly more salamanders, Desmognathus fuscus fuscus, displaced downstream returned home than did the animals displaced upstream. A negative geotactic response was not considered by these researchers, who suggested that the salamanders were utilizing either a rheotropic mechanism (orientation to currents) or olfaction in their homing along streams. Any evidence for the use of positive geotaxis in orientation of reptiles or amphibians is also scarce. When released in unfamiliar territory, Bufo bufo (Eibl-Eibesfledt, 1950) and Rana clamitans (Oldham, 1962) respond by moving downhill. Slope of terrain had no effect on homing in American toads, Bufo americanus (Oldham, 1966), salamanders, Plethodon cinereus (Kleeberger and Werner, 1982), or wood turtles, Clemmys insculpta (Barzilay, 1980). Tests in a circular arena showed no difference in orientation between uphill and downhill conditions in painted turtles, Chrysemys picta (Emlen, 1969).

In this study there was little evidence that S. jarrovi used geotaxis, either positive or negative, as a homing mechanism. Male lizards homed equally well from both displacement directions (Table 5), indicating no effect of slope on homing success. More female lizards returned home from displacements up the canyon than down the canyon, although the difference was not significant. This suggests a possible influence of gravitational cues on female homing. Since half of the females displaced downhill returned home, however, it is not likely that females simply move downhill until they reach their home ranges.

Successful homing might also be explained if displaced animals retain a memory of the sensory cues obtained during the displacement journey. During this study an attempt was made to eliminate all visual and olfactory cues from the lizards during displacement by placing them in sealed plastic bags within a heavy cloth bag. The relatively high homing success rate in S. jarrovi indicates that the use of visual or olfactory cues obtained during the displacement journey is an unlikely homing mechanism in this species.

The procedure used to block visual and olfactory cues would not block the reception of cues useful for inertial navigation, a Type III mechanism in which animals might detect all the turns and accelerations of their displacement journey and then use these to calculate the route home. This mechanism cannot be ruled out since it was not directly tested in this project. Further discussion of this mechanism will be included in the section on radio-tracking studies.

The fate of non-homers should be taken into consideration when analyzing homing results. Of the 108 normal *S. jarrovi* displaced during the three years of this study 26 were never sighted again. These lizards may have failed to home due to predation. Lizards displaced from their home range would not have the benefit of established escape routes to avoid predators as they might within their home range. Weintraub (1970) suggested that the high rate of disappearance of *S. orcutti* during the first 20 days after release may have been due to predation.

Another possible fate of non-homers is that individuals remain near their release point and establish a new home range. Recaptures of normal lizards in the years following their displacement indicated that 15 lizards had established new home ranges in the area of their release. Nine of these animals were juveniles when displaced while three were one year olds, indicating that younger lizards are more likely to remain in the new area. The establishment of a new home range at the release site also seems to have occurred in some *S. orcutti* (Weintraub, 1970) and *Uta stansburiana* (Spoecker, 1967).

The adaptive significance of homing in animals that routinely travel long distances between home sites and breeding areas, such as birds, turtles, salamanders and frogs, is generally recognized. But why should relatively sedentary species like lizards, particularly *S. jarrovi*, possess a well-developed homing ability? Barthalmus and Bellis (1972) suggest that the mechanisms employed in the homing of non-migratory species are simply those used on a daily basis in maintaining and locating specific areas within their home range. It seems more likely, however, that occasional natural displacements, either voluntary or forced, contribute to the selection of a homing response.

Krekorian (1977) has suggested that predatory chases of individual lizards to areas outside of their home ranges could be a selective factor. Since one of the proposed advantages of home range maintenance is the knowledge of escape routes, however, predatory chases to areas hundreds of meters outside of a lizard's home range are probably very rare. Voluntary excursions away from the home range might also contribute to the selection of homing behavior. Ruby (1978) found that male _S. jarrovi_ are more active and wander longer distances during the fall breeding season than during either the spring or summer.

It is also likely that the annual migration of lizards between their summer and winter ranges, as seen in _S. jarrovi_ (Ruby, 1977; Bissinger, unpublished data) and _S. orcutti_ (Weintraub, 1968), has contributed to selection for orientation and navigation mechanisms. Migrating lizards would need reliable navigation mechanisms to find the winter area and then consistently return to the same summer home range year after year. Homing lizards could use the same orientation mechanisms that are utilized during these yearly migrations.

Whatever the underlying selection factors have been for this behavior, this study has shown a well-developed homing ability in the lizard, _S. jarrovi_, which appears similar to that of most other iguanid lizards studied. While the study of the homing behavior of normal lizards has managed to eliminate some possible homing mechanisms from consideration it has not directly addressed the question of underlying orientation mechanisms. Weintraub's (1970) study of _S. orcutti_ is the only previous attempt to determine the homing mechanism of a lizard. He tested the orientation of animals following displacement in a circular apparatus. The orientation of the lizards was towards the position of the sun instead of towards home. Thus, prior to this study, the homing mechanism had not been successfully studied in even one species of lizard.

Tests of the homing mechanism of S. jarrovi constitute the rest of this study and discussion of these results follows.

B. Parietal Eye and Homing

The results of the displacement experiments indicate that the parietal eye is important in S. jarrovi homing (Table 9). Sixty-one percent of the normal lizards and 57 percent of the sham lizards returned home, while only 20 percent of the experimental lizards successfully homed. These results are consistent with the hypothesis that the parietal eye is an extraoptic photoreceptor used in orientation behavior but by themselves the results do not constitute an adequate verification of the hypothesis. The lower homing success of the experimental lizards could be due to factors other than an inability to orient. These alternate explanations must be explored before a conclusion can be reached regarding the role of the parietal eye in homing orientation.

One alternate hypothesis is that the lower homing success of experimental lizards might be due to a higher proportion of one year old lizards in this treatment group. Since younger lizards were previously shown to have a lower homing success than older lizards, this could bias the homing results if not taken into consideration. This possibility can be ruled out, however, since approximately 50 percent of the lizards displaced in each parietal eye treatment group were one year olds (Table 11). Thus, any effect of lizard age would have been consistent among the three groups.

The relatively high proportion of one year old lizards in the initial displacement studies, however, could account for the differences noted in homing success between the early displacement studies and the later radio-tracking studies. One hundred percent of all normal and sham lizards displaced during the radio-tracking experiments successfully homed within two days. Since transmitters could only be implanted in larger lizards, all radio-tracked lizards were at least two years of age and most were older. Thus, the groups of lizards utilized in the radio-tracking studies would be expected to have a higher homing success rate than the previous displacement groups in which young lizards constituted 50 percent of the sample size.

Disruption of the general behavior patterns of lizards following parietal eye treatment might also explain the lower homing success of the experimental lizards. Previous researchers have demonstrated various behavioral changes in several species of iguanid lizards following parietalectomy or parietal eye shielding. Increases in activity levels have been noted in S. occidentalis (Stebbins and Eakin, 1958) and Xantusia vigilis (Glaser, 1958) following parietal eye treatment. Heightened activity for lizards of both species in which the parietal eye had been treated was shown by increases in daily mobility. This resulted in larger movements from previously determined home ranges in S. occidentalis (Stebbins and Eakin, 1958). Any such increased activity in S. jarrovi would tend to increase energy expenditures (Bennett and Dawson, 1976) and might hinder the ability of a lizard to embark on a homing journey that would incur an additional energy cost. The activity levels of S. jarrovi were monitored throughout this study to check for the possibility of altered activity levels in experimental animals. Since S. jarrovi individuals are not always active every day (Simon and Middendorf, 1976) the mean number of days per week that lizards were sighted was used an an indication of their activity levels. Data from control animals which remained in their home ranges indicated no significant differences in this measure of activity among the three parietal eye treatment groups (Table 8).

Home range size is an indirect measure of activity since it is possible that lizards with higher levels of activity will move greater distances in the same amount of time than less active lizards. The home ranges of control lizards were measured and no significant effect of parietal eye treatment was noted (Figure 4, Table 6). Taken together the home range and activity data suggest that shielding the parietal eye did not affect activity in S. jarrovi and would not be a good explanation of the poor homing success of the experimental lizards.

Stebbins and Eakin (1958) suggested that parietalectomy might lead to a lower life expectancy in lizards. Their reasoning was based on three lines of evidence: 1) the increased activity levels of parietalectomized lizards would heighten energetic expenditures, thus shortening the life span. 2) Parietalectomized lizards displayed a lower inclination to move upon the approach of a researcher. This behavior, if extrapolated to the lizard's reaction to a predator, might lead to higher predator losses. 3) Parietalectomized lizards spent more time exposed in full sunlight than the controls. In a year and a half of observations, however, parietalectomized S. occidentalis were not shown to survive at a lower rate than sham-operated lizards (Stebbins and Eakin, 1958). The survivorship of S. jarrovi following parietal eye treatment also showed no significant differences among the three treatment groups (Tables 7 and 12). This was true of the control animals which remained in their home ranges as well as the displaced lizards. These results indicated that the lower homing success of the experimental lizards is not due to lower survival of that group.

Another possible result of the manipulation of the parietal eye is the disruption of thermoregulation. Numerous laboratory studies have documented the selection of higher body temperatures by parietalectomized lizards (reviewed in Ralph, Firth and Turner, 1979; Ralph _et_ _al_., 1979). Since lizard metabolism is dependent upon temperature (Bennett and Dawson, 1976) the maintenance of higher body temperatures by parietalectomized lizards would result in increased energetic costs, and these costs might interfere with successful homing. In addition, the maintenance of higher body temperatures could affect other aspects of normal behavior, and this might disrupt homing.

Field studies on several species of lizards have shown that shielding the parietal eye results in increased exposure of animals to direct sunlight (Stebbins and Eakin, 1958; Stebbins, 1963; Packard and Packard, 1972). It seems logical that lizards which spend more time in the sun would have higher body temperatures, but such was not the case for _S_. _occidentalis_ (Stebbins and Eakin, 1958). Removal of the parietal eye did not result in the selection of higher body temperatures in this species.

A field study of the effect of parietalectomy on energy expenditure in _S_. _occidentalis_ showed no significant differences between the metabolic rates of parietalectomized, sham-operated or intact groups (Bickler and Nagy, 1980). This suggests that body temperatures were not elevated in the parietalectomized lizards. Thus, despite clear evidence of the selection of higher temperatures by parietalectomized lizards in the laboratory, results from field studies are less clear.

The evidence obtained on S. jarrovi thermoregulation during this study (to be discussed in detail later) indicates that shielding the parietal eye does not influence body temperatures over a time period of two to four days (Tables 17 and 18). Since all normal and sham lizards returned home within two days, these results make it unlikely that the poor homing success of the experimental lizards can be interpreted as a result of any disruption in thermoregulatory behavior.

In summary, shielding of the parietal eye was not found to affect S. jarrovi survivorship, daily activity, home range size or thermoregulation. It is therefore unlikely that the lower homing success of the experimental lizards is caused by a disruption of normal activity and thermoregulatory behavior following shielding of the parietal eye.

The radio-tracking data provide additional evidence in support of the hypothesis that the parietal eye is directly involved in the homing orientation of S. jarrovi. Several measures of the homing orientation of displaced S. jarrovi indicated that the experimental lizards could not orient towards home while the normal and sham lizards could. As noted above, 100 percent of the normal and sham lizards returned home within two days after displacement while no experimental lizards returned home. Similarly, the return pathways of all normal lizards as well as 12 of 14 sham-treated lizards were oriented (Table 13), as was shown by Hodges-Anje tests. By contrast no pathways of experimental animals were oriented. In addition, Hotelling T^2 tests showed that the pathways of normal and sham-treated groups were significantly oriented towards home (Figure 11). The pathways of experimental lizards, however, were not oriented in the predicted direction. Analysis of the initial orientation of lizards 30 minutes after release also showed an effect due to parietal eye treatment. Both sexes of normal lizards as well as female sham-treated lizards were significantly oriented towards home while male shams were not (Figure 12, Table 14). At the same time both sexes of experimental lizards moved randomly immediately after release. The sham males showed significant improvement in their orientation over time while the experimental animals did not. Collectively all of these results indicate that the parietal eye is necessary for homing orientation in S. jarrovi.

Except for the differences in orientation towards home the behavior of the experimental lizards was similar to that displayed by the normal and sham-treated lizards. All individuals in each of the three treatment groups of displaced lizards maintained a high level of activity. Each day all lizards became active shortly after the time that the sun's rays hit their overnight locations. They would emerge from their resting locations and bask in full sunlight until their body temperatures reached levels associated with normal activity (approximately 34 to 37°C). The normal and sham lizards then began to move towards home while the experimental lizards wandered considerable distances in the area near their release site. Such high levels of activity are not common in S. jarrovi during the summer months (Simon and Middendorf, 1976; Ruby, 1978; Bissinger, personal observations). Individual S. jarrovi are usually very sedentary, moving infrequently and traveling short distances when they do move. Ruby (1978) found that the mean distances moved per day by S. jarrovi ranged from 12.8 m to 28.6 m during the summer months. All displaced lizards, whether normal, sham or experimental, traveled distances considerably greater than this each day that they were radio-tracked. These data suggest that all displaced lizards were attempting to return home.

Barzilay (1980) suggested three possible reasons why healthy animals might not home: 1) animals might be unable to home because cues were unavailable, 2) animals might be unable to home because they could not make use of available cues, and 3) they might not home due to lack of motivation.

These possible explanations of non-homing will now be discussed for S. jarrovi. In every release of male lizards equipped with transmitters, three animals were displaced simultaneously with one lizard in each parietal eye treatment group. Female lizards were released six at a time, with two lizards in each group. The normal and sham-treated lizards always traveled towards home while the experimental animals moved randomly. It thus appears that homing cues were available to the lizards upon release. Since the experimental animals were released within the same study site and within a short time of the normal and sham animals, it is probable that the same homing cues were also available to them. It therefore seems unlikely that the experimental animals did not home due to an absence of orientational cues.

There is no evidence to support a lack of motivation as a reason for the failure to home of the experimental lizards. Of the 14 experimental lizards released none returned home, even though six of them had previously homed successfully. Additionally, all of these displaced lizards were two years of age and older. Older lizards had previously been shown to home more successfully (Table 4), probably as a result of a stronger attachment to their home ranges and territories. It seems unlikely that the motivation of experimental lizards to return home was any less than that of the normal and sham animals.

It thus appears that the experimental lizards did not orient towards home because they could not make use of the orientational cues that were available to the normal and sham animals. Instead of moving toward home the experimental lizards that were radio-tracked during 1982 spent considerable energy moving randomly about the area surrounding their release points (Figure 10). This extensive random movement could possibly explain why 20 percent of the experimental lizards in the 1979 and 1980 displacement studies were recorded as successful homers. The mean time of 7.25 days recorded for these lizards to return home would seem to be sufficient for animals to return home by random wandering, a homing mechanism proposed by Griffin (1952).

Prior to the radio-tracking studies random wandering by displaced S. jarrovi could not be verified for any treatment group since the pathways taken by homing lizards, as well as the exact homing times, were unknown. The pathways obtained via telemetry, however, indicate that this is not the method by which normal S. jarrovi homed. Most normal and sham lizards traveled along oriented pathways following displacement (Figures 6 and 7). Since the experimental radio-tracked lizards traveled considerable distances while moving randomly after displacement it is possible that some of these animals could have returned home given enough time. If radio-tracking had been carried out for a longer period of time I would have expected one or more of these experimental lizards to eventually return home. This seems likely because three of the 14 experimental lizards had moved approximately 50 m towards home by the end of the second day of radio-tracking.

Barzilay (1980) suggested that initial orientation was difficult for wood turtles, Clemmys insculpta. She found that approximately half of the untreated wood turtles initially headed in directions away from home and later changed their headings to a more homeward course. A similar phenomenon seemed to occur in S. jarrovi homing. The two sham-treated lizards whose pathways were not significantly oriented by the Hodges-Anje test (Figures 8 and 9) initially traveled in inappropriate directions as though disoriented. Within two and one-half hours of their release, however, both lizards had corrected their orientation and were traveling in a homeward direction. This correction in the early hours after release is also shown in the initial orientation of the male sham-treated lizards, which was not homeward oriented 30 minutes after release but by three and one-half hours after release was significantly homeward oriented (Figure 13). Thus, it appears that, at least occasionally, initial orientation is more difficult for some lizards.

A possible homing mechanism that could not be adequately tested prior to my use of telemetry is inertial navigation. An animal could return home while using an inertial guidance system in two different ways: 1) it might simply retrace the route of its displacement journey, or 2) it might integrate all the linear and angular accelerations and then compute the direct route home. The first possibility is easily ruled out by following the routes of the animals after their release. The second possibility is harder to eliminate and was not investigated during my study of S. jarrovi homing.

Inertial guidance has been suggested as a mechanism by which animals home (Darwin, 1873; Barlow, 1964). Numerous experiments on pigeons, however, have ruled out homing by the retracing of the displacement route (reviewed in Keeton, 1974). The second possibility has been tested indirectly many times. Birds have been carried to release sites while being rotated (Griffin, 1940) and while under deep anesthesia (Walcott and Schmidt-Koenig, 1973). In addition, the presumed detectors of accelerations, the vestibular organs, have been lesioned in pigeons prior to release (reviewed in Keeton, 1974). The results of these experiments have been consistently negative, although such negative evidence cannot absolutely rule out the possibility of inertial guidance in pigeons.

During the radio-tracking study of S. jarrovi homing the first type of inertial guidance (the retracing of the outward journey) was investigated indirectly. All male lizards were carried on circuitous routes within the study area during the displacement journey. The females, however, were carried on a complex journey. They were captured in the South Fork study site, carried by foot and motor vehicle to the Southwestern Research Station where they underwent surgery for the implantation of a transmitter, and then subsequently returned to South Fork for release at their displacement sites. Since all normal and sham lizards returned home in fairly direct pathways (Figures 6 and 7), there is no evidence that lizards were using an inertial guidance mechanism to retrace their displacement route. Thus, the first type of inertial navigation can be eliminated as the homing mechanism used by S. jarrovi. This study did not investigate the use of the integration method of inertial guidance in S. jarrovi homing. The fact that lizards with shielded parietal eyes were disoriented, however, is not consistent with an inertial guidance mechanism since it is not likely that the parietal eye could be a receptor of the cues used in this mechanism.

The use of learned visual landmarks is a frequently discussed homing mechanism (Baker, 1978). Weintraub (1970) suggested that S. orcutti relied upon visual landmarks to return home. Tracks of displaced painted turtles, Chrysemys picta, indicated that the turtles were orienting towards a tree-line (Emlen, 1969). Landmark recognition has been suggested as the basis of homing in Mexican toads, Bufo valliceps (Grubb, 1970) and American toads, Bufo americanus (Oldham, 1966).

During this study S. jarrovi individuals were always displaced well outside their summer home ranges and presumably in unfamiliar territory. While some animals may be familiar with a larger area due to past emigrations it is unlikely that most lizards could have oriented on the basis of learned visual landmarks on their first release. Lizards that were released more than once at a given displacement site, however, might be expected to return home by using learned visual landmarks. Four experimental radio-tracked S. jarrovi were displaced at release sites from which they had previously homed. None of these animals returned home after these second displacements. If learned visual landmarks alone were generally used by homing S. jarrovi these lizards could have returned home instead of wandering randomly about the release site. It is possible, however, that displaced S. jarrovi could utilize learned visual landmarks in conjunction with a compass sense to return home. In such a situation the landmarks alone would not be sufficient to guide a lizard home if it could not perceive the necessary compass cues. Shielding the parietal eye of the experimental lizards might interfere with the reception of celestial cues needed for sun-compass orientation.

All of the above observations reinforce the hypothesis that the parietal eye is an important receptor in _S. jarrovi_ homing orientation. This is the first study to show that lizards are capable of orienting via an extraoptic photoreceptor. Since this is also the first detailed investigation of a homing mechanism in any species of lizard, it is not possible at this time to discuss these results in relation to the mechanisms used by other species. Comparison can be made, however, with the research on amphibian orientation.

Extraoptic photoreceptors (EOPs) have been shown to be used, either exclusively (Adler and Taylor, 1973) or in concert with ocular receptors, in the compass orientation of amphibians (reviewed in Adler, 1976). The EOPs implicated in this response are the pineal organ in salamanders and both the pineal and frontal organs in frogs. Since the parietal eye of lizards is thought to be homologous to the frontal organ of frogs (Ariens-Kappers, 1965) it is very possible that the two organs might have similar functions. This study of _S. jarrovi_ homing does not provide any clear evidence of a role for the pineal gland in homing. The experimental lizards all had intact pineal glands but were not able to orient towards home, suggesting that any cues received by the pineal organ were not sufficient for homing orientation. It is possible, however, that the pineal is involved in orientation via its neural connections with the parietal eye. Any such role of the pineal gland was not investigated in this study.

It also appears that the lateral eyes alone are not capable of utilizing the necessary cues for the orientation of S. jarrovi. If they were the lizards with shielded parietal eyes would have oriented as well as the normal lizards. This does not necessarily mean that the eyes are unimportant in S. jarrovi homing. It does indicate, however, that cues must be available to the parietal eye for successful orientation to occur. The present study did not produce evidence that the parietal eye alone is capable of mediating orientation, since no lizards were deprived of their normal vision. Such tests were not conducted during this study because I believed that blind lizards would not survive very long in the field. Iguanid lizards are dependent on vision for most of their daily activities. Blind lizards would not be able to locate and capture prey, avoid predators, or defend their territories.

I suggest that in S. jarrovi the parietal eye is utilized in a sun-compass orientation response which aids the lizards in homing. Evidence of sun-compass orientation and further discussion of this topic will be presented in the next section.

C. Parietal Eye and Sun-compass Orientation

This study clearly demonstrated that S. jarrovi can use a time-compensated, sun-compass mechanism to orient to a home area. The compensation exhibited in the lizards' orientation after phase-shifting shows the possession of an internal biological clock which can be synchronized by the local light-dark cycle. The normal lizards exhibited the expected counter-clockwise shift in orientation following the six hour phase advance (Figure 14), thus indicating a sun-compass mechanism of orientation.

Sun-compass orientation has been studied in amphibians (reviewed in Ferguson, 1971) and the following reptiles: turtles (DeRosa and Taylor, 1978, 1982), water snakes (Newcomer, Taylor and Guttman, 1974), and alligators (Murphy, 1981). This research has clearly demonstrated the use of a sun-compass in Type II, or Y-axis, orientation. Such orientation is not towards home but instead towards a learned compass direction, such as the direction to the shoreline in wild-caught animals or to a trained direction in captive animals. Similar studies of the lacertid lizard, Lacerta viridis, suggest that lizards trained to a particular direction are capable of using celestial cues for orientation (Fischer, 1961; Fischer and Birukow, 1963).

While a sun-compass is clearly involved in these natural movements to shorelines or other landmarks within the home area of an animal, the role of a sun-compass in displacement studies of amphibians and reptiles is less well understood. No definitive evidence exists that a sun-compass is used in homing orientation of amphibians and reptiles, since the critical phase-shift experiments which would be necessary to demonstrate such orientation have not been performed. Other evidence, however, suggests that some species may be able to use a sun-compass to orient towards home after displacement. The tailed-frog, Ascaphus trueii, can orient towards home after displacement in an open container while southern cricket frogs, Acris gryllus, cannot (Ferguson, 1971). Landreth and Ferguson (1967) reported orientation towards the breeding pond in rough-skinned newts, Taricha granulosa, following displacement. Ferguson (1971), however, suggested that most species of amphibians return home after displacement by using cues other than those employed in sun-compass orientation.

Studies on displaced reptiles have produced results that are contradictory and somewhat conflicting. Gould (1957, 1959) found that displaced box turtles, Terrapene carolina, and painted turtles, Chrysemys picta, oriented correctly under sunny skies and incorrectly under overcast skies. He also found that when a mirror was used to change the apparent direction of the sun, the box turtles altered their orientation in the predicted direction. Emlen (1969) found that displaced painted turtles were able to return home from distances as far as 100 m from their pond. This ability persisted under overcast conditions, however, indicating that celestial cues were not essential in orientation. Similarly, displaced wood turtles, Clemmys insculpta, were as well oriented under complete overcast as they had been under sunny skies (Barzilay, 1980).

While much of this research on amphibians and reptiles is suggestive of a role of a sun-compass in homing orientation, as pointed out before the definitive phase-shifting experiments had not been performed. All previous phase-shifting experiments on reptiles and amphibians had been conducted in artificial arenas with animals trained to orient in certain directions. Phase-shift experiments on the natural homing orientation of amphibians and reptiles had not been attempted. Thus, my study of the orientation of S. jarrovi provides the first unequivocal evidence of the use of a sun-compass in reptilian homing orientation.

The demonstration of the use of a sun-compass, however, does not satisfactorily explain how animals can return home after displacement. In simple Type II orientation a sun-compass enables an animal to move in a consistent, learned direction following release. Such orientation will result in homing only when animals are displaced in directions 180°

opposite to their preferred direction. An animal displaced in any other direction will not return home if it simply moves in the previously learned direction. The ability to orient in a consistent compass direction is of no help in homing if an animals does not know the home direction. Kramer (1953) pointed out that an animal displaced to an unfamiliar area probably needs both a "map" sense to determine the direction towards home, and a compass to find that direction. A sun-compass by itself, therefore, is rarely sufficient for homeward navigation in an animal displaced to unfamiliar territory.

Numerous experiments have shown the importance of the sun in bird orientation and homing (reviewed in Keeton, 1974; Emlen, 1975). A large body of evidence has demonstrated that the sun, when available, plays a primary compass role in homing pigeons and diurnally migrating birds. The "map" sense of these birds, however, has proven more difficult to understand (Gould, 1982). In principle, the sun could provide the necessary map information as well as serving as a compass. Matthews (1953, 1955) proposed a theory of complete bicoordinate navigation by the sun alone, the 'sun arc' hypothesis. He suggested that a bird could use the sun's elevation and arc in combination with their own internal time sense to determine the direction it must fly to get home. Research on the explicit, testable predictions of Matthew's hypothesis, however, has failed to find any support for the hypothesis. The most important evidence against the hypothesis comes from the results of clock-shift experiments. The bearings chosen by clock-shifted birds are regularly consistent with the use of the sun as a simple compass but they are not consistent with Matthew's hypothesis. In addition, theoretical considerations have made the 'sun arc' hypothesis seem very unlikely. The theory requires that an animal possess extraordinary accuracy of vision in measuring the sun's altitude, azimuth, and angular motion, as well as an extremely accurate biological clock. A timing error of only two to three minutes might preclude the use of bicoordinate navigation at displacement distances of less than 40-50 km since the position-finding error is likely to be greater than these distances (Emlen, 1969). Neither the visual acuity or the biological clocks of pigeons have been shown to possess the accuracy needed for this type of navigation (reviewed in Keeton, 1974). Thus, while there is abundant evidence showing that birds use the sun as a compass there is little support for the idea that the sun provides accurate information about the precise direction towards home.

The data on S. *jarrovi* homing orientation show that these lizards are interpreting the six hour advanced phase-shift as a compass rotation and not as a map displacement. Animals utilizing 'sun arc' navigation should interpret a six hour phase advance as a very long displacement, one quarter of the way around the world to the west. Hence lizards released in any direction from home should have oriented towards the east. Assuming the use of the sun as a compass, however, results in very different predictions. In an experimental situation where a lizard's biological clock has been advanced six hours, all animals should shift their orientation 90° counterclockwise from home. This is exactly what the results of the phase-shifting experiments on S. *jarrovi* showed (Figure 14). The phase-advanced lizards displaced down the canyon (north) oriented towards the east while those displaced up the canyon (south) oriented towards the west. These results are consistent with the use of the sun as a compass while they contradict the hypothetical use of the sun in bicoordinate navigation. Thus, it seems likely that S. jarrovi are using the sun solely as a directional cue for maintaining their homeward orientation.

The evidence showing the use of a sun-compass in S. jarrovi homing orientation suggests that these animals are using a homing system comparable to Kramer's map-and-compass model. According to this model, a displaced animal first determines its geographical location relative to home from some unknown source (the map step), and then it merely uses the sun as a compass to move in the direction needed to return home (the compass step). I suggest that S. jarrovi are using some unknown cues to determine the direction of displacement from home prior to using a sun-compass to locate the deduced homeward direction.

The results of this study implicate the parietal eye, and not the lateral eyes, as the critical receptor for the perception of the celestial cues utilized in this sun-compass response. If the eyes alone were capable of utilizing these cues the experimental lizards maintained on the natural day-night cycle should have oriented towards home while the experimental lizards that were phase-shifted should have changed their direction of orientation in the predicted direction. The results showed instead that both groups of experimental lizards moved randomly after displacement, suggesting that the necessary cues were not available to these lizards.

What function could the parietal eye serve in lizard orientation that would not also be performed by the lateral eyes? It is possible that the lizard parietal eye is useful in orientation by acting as a highly specialized analyzer of the e-vector of polarized light (Adler, personal communication). The e-vector of linearly polarized light can be used for compass orientation since it bears a fixed relationship to the sun's position (Sekera, 1957). Several kinds of evidence support the hypothesis that the parietal eye is a receptor for polarized light. The photoreceptors in the parietal eye are arranged in a pattern such that many are in a plane perpendicular to overhead light (Hamasaki and Eder, 1977). This arrangement of the photoreceptors should theoretically allow for the analysis of polarized light. Denton (1959) has shown that the absorption of linearly polarized light in the outer segment of the photoreceptors of frogs is independent of the bearing of the e-vector for light passing axially through the outer segment. This is the ordinary bearing of light passing through the outer segment of the photoreceptors of the lateral eyes. When light passes transversely (perpendicular to the long axis of the receptors), however, the amount of absorption is directly related to the bearing of the e-vector.

If these absorption properties also exist for the photoreceptors of the lizard parietal eye, it is possible that lizards could perceive the polarization patterns available in the sky and use them in orientation. Such a mechanism would be consistent with the data showing that the use of the lateral eyes alone is not sufficient for sun-compass orientation in *S. jarrovi*.

Many species of invertebrates are capable of perceiving polarized light and using it in spatial orientation (reviewed in von Frisch, 1967; Waterman, 1973). The number of species of vertebrates that have demonstrated such a polarotactic ability are much more limited but the list is continually growing and now includes several species of fish (Waterman and Forward, 1971; Dill, 1971; Forward and Waterman, 1973; Kleerekoper *et* *al*., 1973; Davitz and McKaye, 1978), pigeons (Kreithen and Keeton, 1974; Delius, Perchard and Emmerton, 1976), salamanders (Taylor and Adler, 1973), and frogs (Auburn and Taylor, 1979).

Of particular relevance to this study of *S*. *jarrovi* orientation is the discovery that the ability of some of these species to orient to polarized light cues depends upon an EOP. When opaque plastic was inserted over the skulls, but not the eyes, of tiger salamanders, *Ambystoma* *tigrinum*, the animals failed to orient whether they were sighted or eyeless (Adler and Taylor, 1973). Outdoor tests of bullfrog tadpoles, *Rana* *catesbiana*, also indicated that the reception of linearly polarized light does not reside in the eyes, but probably is associated with the pineal complex. Adler (personal communication) has shown in recent tests with *Uma* *notata* that shielding the parietal eye prevented the lizards from orienting polarotactically.

The data showing that the lateral eyes are not involved in the sun-compass orientation of *S*. *jarrovi*, along with the anatomical and behavioral evidence presented above, suggest that *S*. *jarrovi* may be capable of orienting to polarized light. Adler (1976) summarized the instances when the ability to detect the e-vector would be of adaptive value to animals. Such cues should be useful in the following situations where the sun cannot be perceived directly: 1) underwater,

2) during twilight, and 3) in forested areas where the view of the sun might frequently be obstructed. In the wooded canyon where this study of *S. jarrovi* homing was conducted the view of the sun is often blocked by trees, boulders, and the canyon walls. An ability to detect the e-vector of polarized light would allow these lizards to infer the position of the sun as long as an unclouded patch of blue sky was available. Thus, orientation would not be restricted to times when the sun was directly visible.

Specific experiments need to be designed to test for the possibility that *S. jarrovi* are orienting to polarized light during their homing journeys.

D. Parietal Eye and Thermoregulation

Although parietalectomy or parietal shielding in several species of lizards has been shown to result in their remaining exposed to light for increased periods of time (Stebbins and Eakin, 1958; Stebbins, 1963, 1970; Stebbins and Wilhoft, 1966; Packard and Packard, 1972), as well as their selection of higher body temperatures (Hutchison and Kosh, 1974; Engbretson and Hutchison, 1976; Roth and Ralph, 1976, 1977; Phillips and Harlow, 1981), this study did not show any overall changes in *S. jarrovi* thermoregulation after shielding of the parietal eye (Figures 16 and 17). These results are consistent, however, with all previous field studies of lizard thermoregulation. Shielding of the parietal eye did not result in the selection of higher body temperatures in free-ranging *S. occidentalis* (Stebbins and Eakin, 1958). Field data on the energy expenditure of *S. occidentalis* indirectly suggest that parietalectomy did not induce changes in body temperature selection by these lizards (Bickler and Nagy, 1980). Parietalectomized lizards were not found to have significantly higher metabolic rates than intact lizards. Since temperature affects the metabolism of lizards it is unlikely that these parietalectomized S. occidentalis were maintaining higher body temperatures.

All of the experiments suggesting that the parietal eye is involved in thermoregulatory behavior have been conducted in the laboratory. The thermal behavior of lizards maintained in photothermal gradients with stationary light and/or heat sources, however, may not closely approximate that of free-living lizards. Such simplified laboratory environments probably do not allow the animals to display a complete range of appropriate behavior, and this may result in a distorted concept of thermoregulation (Avery, 1982). In addition, the activity levels of lizards in small laboratory chambers are probably lower than in free-ranging animals. Lizards in the field need to hunt for prey, avoid predators and defend their territories, a range of behavior much broader than that of captive lizards which simply need to eat the food provided and maintain their body temperatures within the normal range. The temperatures selected by lizards in the laboratory may represent an optimum physiological temperature for the animals. The range of body temperatures at which lizards show such active behavior as hunting, feeding, and fighting is frequently referred to as the activity temperature (Pough and Gans, 1982). The optimum physiological temperature and the optimum activity temperature may not always be the same (Huey and Slatkin, 1976). This difference might lead to differences in the body temperatures selected by lizards in the field versus those selected in the laboratory.

Previous studies have shown such differences between lizard body temperatures measured in the field and the laboratory. The mean body temperature of S. magister recorded in the laboratory was 33.2°C (Engbretson and Hutchison, 1976). This is somewhat lower than the mean temperatures of 34.9°C (Bogert, 1949), 34.8°C (Brattstrom, 1965), 34.3°C (McGinnis and Falkenstein, 1971), and 34.8°C (Parker and Pianka, 1973) measured for this species in the field. Licht et al (1966) also noted such discrepancies between field and laboratory measurements in Australian lizards. A prior laboratory study on S. jarrovi thermoregulation (Bissinger, unpublished data) recorded a mean body temperature of 34.6°C, which is lower than the mean body temperatures of 35.9-36.1°C measured in my field study. It thus may be a general phenomenon that lizards in the field maintain higher body temperatures than those tested in laboratory gradients.

It is possible that such differences in the thermoregulatory behaviors of free-ranging and captive lizards could explain why all laboratory studies show that shielding the parietal eye affects thermoregulation while my study and other field research shown no effect. Untreated lizards in laboratory gradients may maintain body temperatures slightly lower by one to two Celsius degrees than the normal activity temperatures for the same species in the field. When the parietal eye is removed or shielded a thermophilic response occurs which raises the body temperatures of these lizards residing in the laboratory to the range of temperatures typically recorded for free-ranging lizards. This is is distinct possibility in S. magister since the mean body temperatures selected by parietalectomized lizards in photothermal gradients (34.5°C: Engbretson and Hutchison, 1976) are similar to the mean body temperatures recorded for this species via telemetry in the field (34.3°C: McGinnis and Falkenstein, 1971). The recorded differences between the mean body temperatures of intact and parietalectomized lizards of all species is typically only a few degrees. This temperature difference was 1.7°C in S. magister (Engbretson and Hutchison, 1976), and 2.1°C and approximately 3°C respectively in two separate studies of A. carolinensis (Roth and Ralph, 1976; Hutchison and Kosh, 1974). In no case did parietal treated lizards of any species raise their mean body temperatures to extremely high levels near the critical thermal maxima. The temperature gradients utilized in these studies would have permitted lizards to select body temperatures much higher than those selected by the parietalectomized lizards. This suggests that there is a temperature limit to the thermophilic response of these lizards. Free-ranging animals that are already maintaining higher body temperatures would probably be closer to such a limit prior to parietal eye treatment. Lizards released in the field might not select higher body temperatures after parietal eye treatment if such behavior would cause their temperatures to approach uncomfortable or lethal levels.

The results of this study do not completely rule out a role of the parietal eye in S. jarrovi thermoregulation since body temperatures of lizards were only monitored for the first two or three days after parietal eye manipulation. Phillips and Harlow (1981) observed a time lag of four to six days in the elevation of lizard body temperatures after shielding of the parietal eye. It is possible that such an effect may have been shown in S. jarrovi if lizard body temperatures had been recorded for a longer period of time. This was not feasible during this study, however, because time was short and my primary objective was to study the homing orientation of these lizards. My main purpose for monitoring the body temperatures of *S. jarrovi* was to ascertain if there was any disruption of thermoregulation in the experimental lizards that could interfere with their homing orientation. All of the radio-tracked lizards that successfully homed did so within two days, thus the length of time that temperatures were monitored during this study was sufficient for my primary purpose. Since the parietal eye was not shown to affect thermoregulation in *S. jarrovi* over the time period needed for homing, it is very unlikely that a disruption of thermoregulation in the experimental lizards was a factor in their poor homing orientation.

E. Summary and Conclusions

This study has shown that adult *S. jarrovi* are capable of returning to their home ranges after displacement. Since lizards were released well outside their summer home ranges it is unlikely that a direct field of vision back to their home area guided them home. Simple Type II compass orientation can be eliminated as a homing mechanism since lizards homed with similar success when displaced in opposite directions. Also, geotaxis is an unlikely mechanism since lizards returned home when displaced either uphill or downhill. Although the experimental evidence is not sufficient to eliminate inertial guidance as a homing mechanism, it is not a very likely one.

Both the displacement and radio-tracking studies provide evidence that the parietal eye is important in *S. jarrovi* homing. Lizards with shielded parietal eyes were disoriented and returned home in significantly fewer numbers than control animals. These poor homing results do not seem to be due to a general disruption of lizard behavior after parietal eye manipulation since this treatment did not appear to influence lizard activity, home range size, survivorship, or thermoregulation. The data suggest that lizards with shielded parietal eyes did not orient towards home because they could not make use of the appropriate orientation cues. The phase-shifting experiments provide conclusive evidence that *S. jarrovi* utilize a sun-compass mechanism in their initial orientation but cannot do so if the parietal eye is shielded.

It is unlikely that *S. jarrovi* rely solely on cues perceived via the parietal eye when orienting towards home. It is more probable that the parietal eye provides the compass information which is used in conjunction with another "map" sense. The cues underlying this hypothetical "map" sense in *S. jarrovi* are completely unknown at this time, and my study did not address this question. It is possible, however, to speculate what some of these cues might be.

In recent years, two main hypotheses, one based on olfaction and the other on magnetism, have been suggested as the basis of the homing pigeon's "map" sense (reviewed in Gould, 1982). According to the olfactory hypothesis formulated by Papi *et al* (1972) pigeons in their home loft may learn to associate particular odors with winds from certain directions and thus slowly build up an olfactory map of their surroundings. When transported to an unfamiliar territory, the pigeons only have to sniff the air during displacement or at the release site to know the direction of home. To use a magnetic map, on the other hand, pigeons would need to have knowledge of the local rate and direction of magnetic gradients. Upon release they would have to extrapolate from these gradients to determine the distance and direction of displacement. While there is evidence in support of both hypotheses neither one is completely satisfactory as an explanation of the pigeon "map" (Gould, 1982; reply by Wallraff, 1982).

The models developed to explain the map sense of birds may not be directly applicable to the homing over shorter distances performed by lizards. While many discoveries about navigation made with birds have later been shown to apply to other animal groups, it is not wise to overgeneralize. The short distances involved in the homing of small terrestrial vertebrates may preclude the use of some mechanisms used in the orientation of birds. Thus, each general orientation mechanism suggested must be examined both theoretically and/or experimentally in the context of the life history of a particular species.

The possible use of a magnetic compass or "map" sense in reptile and amphibian orientation has barely been investigated. Cave salamanders (Eurycea lucifuga) tested in the laboratory were able to orient with respect to artificial magnetic fields (Phillips, 1977; Phillips and Adler, 1978). Thus, it is possible that these animals can utilize a magnetic compass to orient. Barzilay (1980), however, found no significant difference in various homing parameters between wood turtles wearing electromagnets and control animals. While it is possible that many species can utilize a magnetic compass, the magnetic map hypothesis faces more severe problems, especially for animals displaced very short distances. A seemingly impossible magnetic sensitivity would be necessary for an animal to detect changes in the earth's magnetic field over distances as short as 150 m. It is not known how the nervous system could possibly measure such small intensity variations. While the use of a magnetic map by displaced _S. jarrovi_ is improbable, hypotheses should not be discarded simply because they appear unlikely. Experiments should be designed to test this hypothesis.

While the use of an olfactory map has not been directly tested in amphibians or reptiles, there is evidence that olfactory cues may provide cues for homing orientation in salamanders (Grant _et al._, 1968; Madison, 1969, 1972; Madison and Shoop, 1970; Barthalmus and Bellis, 1972) and in frogs and toads (Martof, 1962; Oldham, 1966; Dole, 1968; Tracy and Dole, 1969; Grubb, 1970). Whether these animals are utilizing an olfactory map or are simply responding to a gradient of site specific chemical cues emanating from their home sites is unknown. Barzilay (1980) suggested that wood turtles, _Clemmys insculpta_, probably rely mainly on olfactory cues to return home. Her data support both an olfactory gradient theory of homing and the Papi hypothesis. The 150 m displacements utilized in the study of _S. jarrovi_ homing did not eliminate the possibility of sensory contact between a displaced lizard and its home range. Directional sensory cues, especially olfactory ones, could have been available to these lizards, and as such could provide information that might aid in homing. This mechanism would be similar to the "intermediate-range homing" mechanism proposed by Carroll and Ehrenfeld (1978) for wood turtles. Since lizards with shielded parietal eyes failed to orient towards home, however, it does not appear likely that olfactory cues by themselves could guide _S. jarrovi_ home. If olfactory cues are important in _S. jarrovi_ homing they probably would provide "map" cues that would be utilized only in conjunction with their compass sense.

Another orientation mechanism that could aid *S. jarrovi* in homing is the use of visual landmarks. The use of only visual landmarks in *S. jarrovi* orientation is unlikely since the experimental lizards were disoriented, and furthermore the phase-shifted lizards shifted their orientation to the predicted direction. Landmarks could, however, be used in conjunction with compass cues to orient in the homeward direction. During this study I displaced lizards to areas well outside their summer home ranges. I believe that most lizards were released in unfamiliar areas and could not have used familiar landmarks to return home. Since I could not observe all the movements of every lizard during all seasons, however, homing by familiar landmarks cannot be entirely ruled out at this time. Experiments could be designed to test for the use of familiar landmarks by displaced *S. jarrovi*. One such experiment would be to release lizards in an arena where they could not see the surrounding landscape and observe their initial orientation behavior. If the animals still oriented in the homeward direction the use of familiar visual landmarks could be eliminated as a possible homing mechanism.

Two other possible cues that could give orientation information to displaced animals are wind direction and acoustic cues (reviewed in Able, 1980). While neither of these could provide animals with absolute compass information both could provide directional cues to homing animals. It is conceivable, although I think unlikely, that such cues could be involved in the "map" sense of *S. jarrovi*. Future research should address these possibilities.

It is not possible to classify the homing behavior of *S. jarrovi* into one of Griffin's (1952) three levels of homing orientation. The exclusive use of piloting (Type I homing) can be excluded because _S. jarrovi_ utilize a sun-compass in their homing orientation. Simple compass orientation by itself (Type II homing) is ruled out because lizards returned home from opposite directions. True navigation (Type III homing) cannot be invoked unless the following criteria are met (Able, 1980): 1) animals must be displaced to areas completely outside of their range of prior experience, and 2) they must be removed to areas where they cannot establish sensory contact with their home. Since _S. jarrovi_ were displaced only 150 m, sensory contact between a lizard and cues from its home range is possible. Thus, _S. jarrovi_ homing does not meet the conditions of Type III homing as defined above. While it is generally possible to classify the orientation behaviors of migrating or homing birds into one of Griffin's three types of homing ability, the same cannot be done for _S. jarrovi_ and probably for most terrestrial vertebrates.

Madison (1972) suggested that Griffin's classification be modified to make it more broadly applicable to other vertebrate groups. He emphasized that fairly sedentary animals could utilize a type of bicoordinate navigation, which he termed "local gradient navigation", by using local gradients instead of the global coordinates suggested for birds. Similarly, Carroll and Ehrenfeld (1978) described the orientation of wood turtles as "intermediate-range homing". Both of these types of homing behavior would include the use of local environmental cues but probably involve something more complex than simple piloting. The same is probably true of _S. jarrovi_ homing. These lizards probably rely on some unknown local cues that provide directional information which is utilized in conjunction with their sun-compass. This is obviously a more complex homing ability than simple piloting, even though it does not quite satisfy the criteria established for Griffin's Type III orientation. *S. jarrovi* homing would be more appropriately described as having similarities to both Type I and Type III homing.

In conclusion, the complete homing mechanisms utilized by *S. jarrovi* are not known at this time, although it is evident that a sun-compass is involved. Future research is needed to determine what cues these lizards are utilizing in conjunction with their sun-compass sense.

V. LITERATURE CITED

Able, K. P. 1980. Mechanisms of orientation, navigation, and homing. In: Animal Migration, Orientation, and Navigation, (S.A. Gauthreaux, Jr., ed.), pp. 283-373. Academic Press, New York. 387 p.

Adler, K. 1968. Extra-optic light entrainment of circadian rhythm in salamanders (Plethodon glutinosus). J. Herp. 2: 176.

Adler, K. 1969. Extraoptic phase shifting of circadian locomotor rhythm in salamanders. Science 164: 1290-1292.

Adler, K. 1970. The role of extraoptic photoreceptors in amphibian rhythms and orientation: a review. J. Herp. 4: 99-112.

Adler, K. 1971. Pineal end organ: role in extraoptic entrainment of circadian locomotor rhythm in frogs. In: Biochronometry, (M. Menaker, ed.), pp. 342-350. U.S. National Acad. Sci., Washington.

Adler, K. 1976. Extraocular photoreception in amphibians. Photochem. Photobiol. 23: 275-298.

Adler, K. and D. H. Taylor. 1973. Extraocular perception of polarized light by orienting salamanders. J. Comp. Physiol. 87: 203-212.

Ariëns-Kappers, J. 1965. Survey of the innervation of the epiphysis cerebri and the accessory organs of vertebrates. In: Progress in Brain Research, Vol. 10: Structure and Function of the Epiphysis Cerebri, (J. Ariens-Kappers and J. P. Schade, eds.), pp. 87-153. Elsevier Publ. Co., Amsterdam.

Auburn, J. S. and D. H. Taylor. 1979. Polarized light perception and celestial orientation in larval bullfrogs Rana catesbeiana. Anim. Behav. 27: 658-668.

Avery, R. A. 1982. Field studies of body temperatures and thermoregulation. In: Biology of the Reptilia, Vol. 12, (C. Gans and F. H. Pough, eds.), pp. 93-166. Academic Press, New York.

Baker, R. 1978. The Evolutionary Ecology of Animal Migration. Holmes and Meier Publ., Inc., New York.

Ballinger, R. E. 1973. Comparative demography of two viviparous iguanid lizards (Sceloporus jarrovi and Sceloporus poinsetti). Ecology 54: 269-283.

Ballinger, R. E. 1979. Intraspecific variation in demography and life history of the lizard, Sceloporus jarrovi, along an altitudinal gradient in southeastern Arizona. Ecology 60(5): 901-909.

Barlow, J. S. 1964. Inertial navigation as a basis for animal navigation. J. Theoret. Biol. 6: 76-117.

Barthalmus, G. T. and E. D. Bellis. 1969. Homing in the Northern Dusky Salamander, Desmognathus fuscus fuscus (Rafinesque). Copeia 1969(1): 148-153.

Barthalmus, G. T. and E. D. Bellis. 1972. Home range, homing and the homing mechanism of the salamander, Desmognathus fuscus. Copeia 1972(4): 632-642.

Barzilay, S. S. 1980. Orientation and homing of the wood turtle (Clemmys insculpta). PhD Thesis, Rutgers University, The State University of New Jersey. 189 p.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. American Institute of Biological Sciences, Washington, D.C. 57 p.

Batschelet, E. 1972. Recent statistical methods for orientation data. In: Animal Orientation and Navigation, (S. R. Galler, K. Schmidt-Koenig, G. Jacobs and R. E. Belleville, eds.), pp. 61-91. National Aeronautics and Space Administration, Washington, D.C.

Batschelet, E. 1978. Second-order statistical analysis of directions. In: Animal Migration, Navigation, and Homing, (K. Schmidt-Koenig and W. T. Keeton, eds.), pp. 3-24. Springer-Verlag, New York.

Bennett, A. F. and W. R. Dawson. 1976. Metabolism. In: Biology of the Reptilia, Vol. 5, (C. Gans and W. R. Dawson, eds.), pp. 127-223. Academic Press, New York.

Bickler, P. E. and K. A. Nagy. 1980. Effects of parietalectomy on energy expenditure in free ranging lizards. Copeia 1980(4): 923-925.

Bogert, C. M. 1949. Thermoregulation and eccritic body temperatures in Mexican lizards of the genus Sceloporus. Ann. Inst. Biol. Mexico 20: 415-426.

Bovet, J. 1972. Displacement distance and quality of orientation in a homing experiment with deer mice (Peromyscus maniculatus). Can. J. Zool. 50: 845-853.

Brattstrom, B. H. 1965. Body temperatures of reptiles. Amer. Midl. Nat. 73(2): 376-422.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160-169.

Brown, J. L. and G. H. Orians. 1970. Spacing patterns in mobile animals. Annual Rev. Ecol. Syst. 1: 239-262.

Calhoun, J. B. and J. U. Casby. 1958. Calculation of home range and density of small mammals. Public Health Monogr. 55: 1-24.

Carpenter, C. C. 1967. Aggression and social structure in iguanid lizards. In: Lizard Ecology, a Symposium, (W. W. Milstead, ed.), pp. 87-106. Univ. Kansas Press.

Carroll, T. E. and D. W. Ehrenfeld. 1978. Intermediate-range homing in the wood turtle, Clemmys insculpta. Copeia 1978: 117-126.

Collin, J. P. 1971. Differentiation and regression of the cells of the sensory line in the epiphysis cerebri. In: The Pineal Gland, (G. E. W. Wolstenholme and J. Knight, eds.), pp. 79-120. Churchill Livingstone, Edinburgh.

Cooke, J. A. and C. R. Terman. 1977. Influence of displacement distance and vision on homing behavior of the white-footed mouse (Peromyscus leucopus noveboracensis). J. Mammal. 58(1): 58-66.

Darwin, C. 1873. Origin of certain instincts. Nature 7: 417-418.

Davitz, M. A. and K. R. McKaye. 1978. Discrimination between horizontally and vertically polarized light by the cichlid fish Pseudotropheus macrophthalmus. Copeia 1978: 333-334.

Delius, J. D., R. J. Perchard and J. Emmerton. 1976. Polarized light discrimination by pigeons and an electroretinographic correlate. J. Comp. Physiol. Psychol. 90: 560-571.

Demian, J. J. and D. H. Taylor. 1977. Photoreception and locomotor rhythm entrainment by the pineal body of the newt, Notophthalmus viridescens (Amphibia, Urodela, Salamandridae). J. Herp. 11(2): 131-139.

Denton, E. J. 1959. The contributions of the oriented photosensitive and other molecules to the absorption of whole retina. Proc. Royal Soc. B 150: 78-94.

DeRosa, C. T. and D. H. Taylor. 1978. Sun-compass orientation in the painted turtle, Chrysemys picta (Reptila, Testudines, Testudinidae). J. Herp. 12(1): 25-28.

DeRosa, C. T. and D. H. Taylor. 1982. A comparison of compass orientation mechanisms in three turtles (Trionyx spinifer, Chrysemys picta and Terrapene carolina). Copeia 1982(2): 394-399.

Dice, L. R. and P. J. Clark. 1953. The statistical concept of home range as applied to the recapture radius of the deermouse (Peromyscus). Contr. Lab. Vert. Biol. 62: 1-15.

Dill, P. A. 1971. Perception of polarized light by yearling sockeye salmon (Oncorphynchus nerka). J. Fish. Res. Bd. Can. 28: 1319-1322.

Dodt, E. and E. Scherer. 1968. Photic responses from the parietal eye of the lizard Lacerta sicula campestris (De Betta). Vision Res. 8: 61-72.

Dole, J. W. 1968. Homing in leopard frogs, Rana pipiens. Ecology 49: 386-399.

Eakin, R. M. 1973. The Third Eye. Univ. Calif. Press, Berkeley.

Eakin, R. M., W. B. Quay and J. A. Westfall. 1961. Cytochemical and cytological studies of the parietal eye of the lizard Sceloporus occidentalis. Z. Zellforsch. 53: 449-470.

Eakin, R. M. and J. A. Westfall. 1959. Fine structure of the retina in the reptilian third eye. J. Biophy. Biochem. Cytol. 6(1): 133-134.

Eakin, R. M. and J. A. Westfall. 1960. Further observations on the fine structure of the parietal eye of lizards. J. Biophys. Biochem. Cytol. 8(2): 483-499.

Eibl, Eibesfeldt, I. 1950. Ein Beitrage zur Paarungsbiologie der Erdkröte (Bufo bufo L.). Behaviour 2(3): 217-236.

Emlen, S. T. 1969. Homing ability and orientation in the painted turtle, Chrysemys picta marginata. Behaviour 33: 58-76.

Emlen, S. T. 1975. Migration: Orientation and navigation. In: Avian Biology, Vol. V, (D.S. Farner, J. R. King and K. C. Parkes, eds.), pp. 129-219. Academic Press, New York.

Engbretson, G. A. and V. H. Hutchison. 1976. Parietalectomy and thermal selection in the lizard Sceloporus magister. J. Exp. Zool. 198: 29-38.

Engbretson, G. A. and C. M. Lent. 1976. Parietal eye of the lizard: Neuronal photoresponses and feedback from the pineal gland. Proc. Nat. Acad. Sci. U.S.A. 73: 654-657.

Ernst, C. H. 1970. Homing ability in the painted turtle, Chrysemys picta (Schneider). Herpetologica 26(4): 399-403.

Ferguson, D. E. 1967. Sun-compass orientation in anurans. In: Animal Orientation and Navigation, (R. M. Storm, ed.), pp. 21-32. Oregon State Univ. Press, Corvallis.

Ferguson, D. E. 1971. The sensory basis of orientation in amphibians. Annals New York Acad. Sci. 188: 30-36.

Ferguson, D. E., J. M. McKeown, O. S. Bosarge and H. F. Landreth. 1968. Sun-compass orientation of bullfrogs. Copeia 1968: 230-235.

Firth, B. T. 1974. Functional aspects of the pineal complex in Lacertilia. PhD Thesis, Univ. of New England, Armidale, Australia.

Firth, B. T. and D. J. Kennaway. 1980. Plasma melatonin levels in the scincid lizard *Trachydosaurus rugosus*. The effects of parietal eye and lateral eye impairment. J. Exp. Biol. 85: 311-321.

Fischer, K. 1961. Untersuchungen zur Sonnenkompassorientierung und Laufaktivität von Smaragdeidechsen (*Lacerta viridis* Laur.). Z. Tierpsychol. 18: 450-470.

Fischer, K. and G. Birukow. 1963. Die Lichtkompassorientierung sonnenlos aufgezogener Smaragdeidechsen (*Lacerta viridus* Laur.). Verh. Dtsch. Zool. Ges. Jena 1963: 316-321.

Fitch, H. S. 1940. A field study of the growth and behavior of the fence lizard. Univ. Calif. Publ. Zool. 44(2): 151-172.

Forward, R. B., Jr. and T. H. Waterman. 1973. Evidence for e-vector and light intensity pattern discrimination by the teleost *Dermogenys*. J. Comp. Physiol. 87: 189-202.

Frisch, K. von. 1967. The Dance Language and Orientation of Bees. Belknap Press, Cambridge, Mass.

Furrer, R. K. 1973. Homing of *Peromyscus maniculatus* in the Channeled Scablands of east-central Washington. J. Mammal. 54: 466-483.

Gauthreaux, S. A., Jr. (ed.). 1980. Animal Migration, Orientation, and Navigation. Academic Press, New York. 387 p.

Glaser, R. 1958. Increase in locomotor activity following shielding of the parietal eye in night lizards. Science 128: 1577-1578.

Goldberg, S. R. 1971. Reproductive cycle of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. Herpetologica 27: 123-131.

Gould, E. 1957. Orientation in box turtles, *Terrepene c. carolina* (Linnaeus). Biol. Bull. 112: 335-348.

Gould, E. 1959. Studies on the orientation of turtles. Copeia 1959: 174-176.

Gould, J. L. 1982. The map sense of pigeons. Nature 295: 205-211.

Grant, D., O. Anderson, and V. Twitty. 1968. Homing orientation by olfaction in newts (*Taricha rivularis*). Science 160: 1354-1356.

Griffin, D. R. 1940. Homing experiments with Leach's petrels. Auk 57: 61-74.

Griffin, D. R. 1952. Bird navigation. Biol. Rev. 27(4): 359-393.

Griffin, D. R. 1978. The sensory physiology of animal orientation. Harvey Lect. 71: 133-172.

Grubb, J. C. 1970. Orientation in post-reproductive Mexican toads, *Bufo valliceps*. Copeia 1970: 674-680.

Guyer, C. 1978. Movement ecology of the short-horned lizard (Phrynosoma douglassi) and the sagebrush lizard (Sceloporus graciosus) in southeastern Idaho. Master's Thesis, Idaho State Univ.

Hamasaki, D. I. 1968. Properties of the parietal eye of the green iguana. Vision Res. 8: 591-599.

Hamasaki, D. I. 1969a. Interaction of the slow responses of the parietal eye. Vision Res. 9: 1453-1459.

Hamasaki, D. I. 1969b. Spectral sensitivity of the parietal eye of the green iguana. Vision Res. 9: 515-523.

Hamasaki, D. I. and E. Dodt. 1969. Light sensitivity of the lizards' epiphysis cerebri. Pflugers Arch. Ges. Physiol. 313: 19-29.

Hamasaki, D. I. and D. J. Eder. 1977. Adaptive radiation of the pineal system. In: Handbook of Sensory Physiology, Vol. VII/5, (F. Crescitelli, ed.), p. 498-548. Springer-Verlag, Berlin.

Harrison, J. L. 1958. Range of movement of some Malayan rats. J. Mammal. 39(2): 190-206.

Huey, R. B. and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62: 991-999.

Huey, R. and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. Quart. Rev. Biol. 51: 363-384.

Hutchison, V. H. and R. J. Kosh. 1974. Thermoregulatory function of the parietal eye in the lizard Anolis carolinensis. Oecologia 16: 173-177.

Ishihara, S. 1969. Homing behaviour of the lizard, Tachydromus tachydromoides (Schlegel). Bull. Kyoto Univ. Educ. Ser. B, No. 36: 11-23.

Jenison, G. L., W. D. Eldred and J. Nolte. 1979. A second class of neurons within the retinas of the parietal eyes of Anolis carolinensis and Iguana iguana. Brain Res. 168(3): 615-618.

Jenison, G. and J. Nolte. 1979. The fine structure of the parietal retinas of Anolis carolinensis and Iguana iguana. Cell. Tiss. Res. 199(2): 235-248.

Jennrich, R. I. and F. B. Turner. 1969. Measurement of non-circular home range. J. Theoret. Biol. 22: 227-237.

Johnson, C. G. 1969. Migration and Dispersal of Insects by Flight. Methuen, London.

Justis, C. S. and D. H. Taylor. 1976. Extraoptic photoreception and compass orientation in larval bullfrogs, Rana catesbeiana. Copeia 1976: 98-105.

Keeton, W. T. 1974. The orientational and navigational basis of homing in birds. Adv. Study Behav. 5: 47-132.

Kleeberger, S. R. and J. K. Werner. 1982. Home range and homing behavior of Plethodon cinereus in northern Michigan. Copeia 1982(2): 409-415.

Kleerekoper, H., J. H. Matis, A. M. Timms, and P. Gensler. 1973. Locomotor response of the goldfish (Carassium auratus) to polarized light and its e-vector. J. Comp. Physiol. 86: 27-36.

Koeppl, J. W., N. S. Slade and R. S. Hoffman. 1975. A bivariate home range model with possible application to ethological data analysis. J. Mammal. 56: 81-90.

Kosh, R. J. and V. H. Hutchison. 1972. Thermal tolerances of parietalectomized Anolis carolinensis acclimated at different temperatures and photoperiods. Herpetologica 28: 183-191.

Kramer, G. 1953. Die Sonnenorientierung del Vögel. Verh. Deut. Zool. Ges. Freiburg, 1952: 72-84.

Kreithen, M. L. 1978. Sensory mechanisms for animal orientation - can any new ones be discovered? In: Animal Migration, Navigation, and Homing, (K. Schmidt-Koenig and W. T. Keeton, eds.), pp. 25-34. Springer-Verlag, New York.

Kreithen, M. L. and W. Keeton. 1974. Detection of polarized light by the homing pigeon, Columba livia. J. Comp. Physiol. 89: 83-92.

Krekorian, C. O'Neil. 1977. Homing in the desert iguana, Dipsosaurus dorsalis. Herpetologica 33(1): 123-127.

Landreth, H. F. and D. E. Ferguson. 1967. Newts: Sun-compass orientation. Science 158: 1459-1461.

Landreth, H. and D. Ferguson. 1968. The sun compass of Fowler's toad, Bufo woodhousei fowleri. Behaviour 30: 27-43.

Lemkau, P. J. 1970. Movements of the box turtle Terrapene c. carolina (Linnaeus) in unfamiliar territory. Copeia 1970: 781-783.

Licht, P. 1971. Regulation of the annual testicular cycle by photoperiod and temperature in the lizard Anolis carolinensis. Ecology 52: 240-252.

Licht, P., W. R. Dawson, V. H. Shoemaker and A. R. Main. 1966. Observations on the thermal relations of western Australian lizards. Copeia 1966: 97-110.

Licht, P. and A. K. Pearson. 1970. Failure of parietalectomy to affect the testes in the lizard *Anolis carolinensis*. Copeia 1970: 172-173.

Madison, D. M. 1969. Homing behaviour of the red-cheeked salamander, *Plethodon jordani*. Animal Behav. 17: 25-39.

Madison, D. M. 1972. Homing orientation in salamanders: A mechanism involving chemical cues. In: Animal Orientation and Navigation, (S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville, eds.), pp. 485-498. National Aeronautics and Space Administration, Washington, D. C.

Madison, D. M. and C. R. Shoop. 1970. Homing behavior, orientation, and home range of salamanders tagged with tantalum-182. Science 168: 1484-1486.

Martof, B. S. 1962. Some observations on the role of olfaction among salientian amphibia. Physiol. Zool. 35: 270-274.

Matthews, G. V. T. 1953. Sun navigation in homing pigeons. J. Exp. Biol. 30: 243-267.

Matthews, G. V. T. 1955. Bird Navigation. Cambridge University Press, London.

Matthews, G. V. T. 1963. The orientation of pigeons as affected by the learning of landmarks and by the distance of displacement. Anim. Behav. 11: 310-317.

Mayhew, W. W. 1963. Biology of the granite spiny lizard, *Sceloporus orcutti*. Amer. Midl. Nat. 69: 310-327.

McGinnis, S. M. and M. Falkenstein. 1971. Thermoregulatory behavior of three sympatric species of iguanid lizards. Copeia 1971: 552-554.

Miller, W. H. and M. L. Wolbarsht. 1962. Neural activity in the parietal eye of a lizard. Science 135: 316.

Murie, M. 1963. Homing and orientation of deer mice. J. Mammal. 44: 338-349.

Murphy, P. A. 1981. Celestial compass orientation in juvenile American alligators (*Alligator mississippiensis*). Copeia 1981(3): 638-645.

Newcomer, R. T., D. H. Taylor and S. I. Guttman. 1974. Celestial orientation in two species of water snakes (*Natrix sipedon* and *Regina septemvittata*). Herpetologica 30: 194-200.

Noble, G. K. 1934. Experimenting with the courtship of lizards. Nat. Hist. 34: 5-15.

Oksche, A. 1971. Sensory and glandular elements of the pineal organ. In: The Pineal Gland (G. E. W. Wolstenholme and J. Knight, eds.), pp. 127-146. Churchill Livingstone, Edinburgh.

Oldham, R. S. 1962. Spring movements in Bufo americanus and Rana clamitans. PhD Thesis, Univ. West. Ontario.

Oldham, R. S. 1966. Spring movements in the American toad Bufo americanus. Can. J. Zool. 44: 63-100.

Packard, G. C. and M. J. Packard. 1972. Photic exposure of the lizard Callisaurus draconoides following shielding of the parietal eye. Copeia 1972: 695-701.

Papi, F., L. Fiore, V. Fiaschi and S. Benvenuti. 1972. Olfaction and homing in pigeons. Monit. Zool. Ital. (N.S.) 6: 85-95.

Papi, F. and H. G. Wallraff (eds.). 1982. Avian Navigation. Springer-Verlag, Berlin.

Parker, W. S. and E. R. Pianka. 1973. Notes on the ecology of the iguanid lizard, Sceloporus magister. Herpetologica 29: 143-152.

Parsons, L. M. and C. R. Terman. 1978. Influence of vision and olfaction on the homing ability of the white-footed mouse (Peromyscus leucopus noveboracensis). J. Mammal. 59(4): 761-771.

Pennycuick, C. J. 1960. The physical basis of astronavigation in birds: theoretical considerations. J. Exp. Biol. 37: 573-593.

Phillips, J. A. and H. J. Harlow. 1981. Elevation of upper voluntary temperatures after shielding of the parietal eye of horned lizards (Phrynosoma douglassi). Herpetologica 37(4): 199-205.

Phillips, J. B. 1977. Use of the earth's magnetic field by orienting cave salamanders (Eurycea lucifuga). J. Comp. Physiol. A 121: 273-288.

Phillips, J. B. and K. Adler. 1978. Directional and discriminatory responses of salamanders to weak magnetic fields. In: Animal Migration, Navigation, and Homing, (K. Schmidt-Koenig and W. T. Keeton, eds.), pp. 325-333. Springer-Verlag, New York.

Pough, F. H. and C. Gans. 1982. The vocabulary of reptilian thermoregulation. In: Biology of the Reptilia, Vol. 12, (C. Gans and F. H. Pough, eds.), pp. 17-23. Academic Press, New York.

Ralph, C. L., B. T. Firth, W. A. Gern and D. W. Owens. 1979. The pineal complex and thermoregulation. Biol. Rev. 54: 41-72.

Ralph, C. L., B. T. Firth and J. S. Turner. 1979. The role of the pineal body in ectotherm thermoregulation. Amer. Zool. 19(1): 273-293.

Rand, A. S. 1967. Ecology and social organization in the iguanid lizard Anolis lineatopus. Proc. U. S. Nat. Mus. 122: 1-79.

Robinson, W. L. and J. B. Falls. 1965. A study of homing of meadow mice. Amer. Midl. Nat. 73(1): 188-224.

Rose, B. 1982. Lizard home ranges: methodology and functions. J. Herp. 16(3): 253-269.

Roth, J. J. and C. L. Ralph. 1976. Body temperature of the lizard (Anolis carolinensis): Effect of parietalectomy. J. Exp. Zool. 198: 17-28.

Roth, J. J. and C. L. Ralph. 1977. Thermal and photic preferences in intact and parietalectomized Anolis carolinensis. Behav. Biol. 19: 341-348.

Ruby, D. E. 1976. The behavioral ecology of the viviparous lizard, Sceloporus jarrovi. PhD Thesis, University of Michigan. 214 p.

Ruby, D. E. 1978. Seasonal changes in the territorial behavior of the iguanid lizard Sceloporus jarrovi. Copeia 1978(3): 430-438.

Ruby, D. E. 1981. Phenotypic correlates of male reproductive success in the lizard, Sceloporus jarrovi. In: Natural Selection and Social Behavior, (R. D. Alexander and D.W. Tinkle, eds.), pp. 96-107. Chiron Press, New York.

Schmidt-Koenig, K. 1964. Initial orientation and distance of displacement in pigeon homing. Nature 201: 638.

Schmidt-Koenig, K. 1983. Orientation. In: Physiology and Behavior of the Pigeon, (M. Abs, ed.). Academic Press, New York.

Schmidt-Koenig, K. and W. T. Keeton (eds.). 1978. Animal Migration, Navigation, and Homing. Springer-Verlag, New York. 462 p.

Sekera, Z. 1957. Polarization of skylight. In: Handbuch der Physik, Vol. 48 (Geophysik II), pp. 288-328. Springer-Verlag, Berlin.

Simon, C. A. 1975. The influence of food abundance on territory size in the iguanid lizard Sceloporus jarrovi. Ecology 56: 993-998.

Simon, C. A. 1976. Territory and home range mapping for lizards and other small animals: A photographic method. Herp. Rev. 7(3): 109.

Simon, C. A. and G. A. Middendorf. 1976. Resource partitioning by an iguanid lizard: Temporal and microhabitat aspects. Ecology 57(6): 1317-1320.

Simon, C. A. and G. A. Middendorf. 1980. Spacing in juvenile lizards (Sceloporus jarrovi). Copeia 1980: 141-146.

Songdahl, J. H. and V. H. Hutchison. 1972. The effect of photoperiod, parietalectomy and eye enucleation on oxygen consumption in the blue granite lizard, Sceloporus cyanogenys. Herpetologica 28: 148-156.

Spoecker, P. D. 1967. Movements and seasonal activity cycles of the lizard Uta stansburiana stejnegeri. Amer. Midl. Nat. 77(2): 484-494.

Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. In: Biology of the Reptilia, Vol. 7, (C. Gans and D. W. Tinkle, eds.), pp. 265-334. Academic Press, New York.

Stebbins, R. C. 1954. Amphibians and Reptiles of Western North America. McGraw-Hill, New York.

Stebbins, R. C. 1960. Effects of pinealectomy in the western fence lizard Sceloporus occidentalis. Copeia 1960(4): 276-283.

Stebbins, R. C. 1963. Activity changes in the striped plateau lizard with evidence on the influence of the parietal eye. Copeia 1963: 681-691.

Stebbins, R. C. 1970. The effect of parietalectomy on testicular activity and exposure to light in the desert night lizard (Xantusia vigilis). Copeia 1970: 261-270.

Stebbins, R. C. and N. W. Cohen. 1973. The effect of parietalectomy on the thyroids and gonads in free living western fence lizards, Sceloporus occidentalis. Copeia 1973: 662-668.

Stebbins, R. C. and R. M. Eakin. 1958. The role of the "third eye" in reptilian behavior. Amer. Mus. Novitates 1870: 1-39.

Stebbins, R. C. and D. C. Wilhoft. 1966. Influence of the parietal eye on activity in lizards. In: The Galapagos. Proceedings of the Symposia of the Galapagos International Scientific Project, (R. I. Bowman, ed.), pp. 258-268. Univ. Calif. Press, Berkeley.

Steyn, W. 1959. Ultrastructure of pineal eye sensory cells. Nature 183: 764-765.

Steyn, W. 1960. Observations on the ultrastructure of the pineal eye. J. Roy. Microscop. Soc. 79: 47-58.

Stickel, L. F. 1949. An experiment on Peromyscus homing. Amer. Midl. Nat. 41: 659-664.

Taylor, D. H. 1972. Extra-optic photoreception and compass orientation in larval and adult salamanders (Ambystoma tigrinum). Anim. Behav. 20: 233-236.

Taylor, D. H. and K. Adler. 1973. Spatial orientation by salamanders using plane polarized light. Science 181: 285-287.

Taylor, D. H. and K. Adler. 1978. The pineal body: Site of extraocular perception of celestial cues for orientation in the tiger salamander (Ambystoma tigrinum). J. Comp. Physiol. A 124: 357-361.

Taylor, D. H. and J. S. Auburn. 1978. Orientation of amphibians by linearly polarized light. In: Animal Migration, Navigation, and Homing, (K. Schmidt-Koenig and W. T. Keeton, eds.), pp. 334-346. Springer-Verlag, New York.

Taylor, D. H. and D. E. Ferguson. 1970. Extraoptic celestial orientation in the southern cricket frog Acris gryllus. Science 168: 390-392.

Tinkle, D. W. 1967. The life and demography of the side-blotched lizard, Uta stansburiana. Misc. Publ. Mus. Zool. Univ. Michigan, No. 132: 1-182.

Tracy, C. R. and J. W. Dole. 1969. Evidence of celestial orientation by California toads (Bufo boreas) during breeding migration. Bull. So. Calif. Acad. Sci. 68(1): 10-18.

Twitty, V. C. 1959. Migration and speciation in newts. Science 130: 1735-1743.

Twitty, V. C., D. Grant and O. Anderson. 1967. Initial homeward orientation after long-distance displacements in the newt Taricha rivularis. Proc. Nat. Acad. Sci. 57: 342-348.

Underwood, H. 1973. Retinal and extraretinal photoreceptors mediate entrainment of the circadian locomotor rhythm in lizards. J. Comp. Physiol. 83: 187-222.

Underwood, H. 1975. Extraretinal light receptors can mediate photoperiodic photoreception in the male lizard Anolis carolinensis.

Underwood, H. 1977. Circadian organization in lizards: the role of the pineal organ. Science 195: 587-589.

Underwood, H. 1981. Parietalectomy affects photoperiodic responsiveness in thermoregulating lizards (Anolis carolinensis). Comp. Biochem. and Physiol. 69A: 575-578.

Underwood, H. and M. Menaker. 1970. Extraretinal light perception: Entrainment of the biological clock controlling lizard locomotor activity. Science 170: 190-192.

Underwood, H. and M. Menaker. 1976. Extraretinal photoreception in lizards. Photochem. Photobiol. 23: 227-243.

Wallcott, C. and K. Schmidt-Koenig. 1973. The effect of anesthesia during displacement on the homing performance of pigeons. Auk 90: 281-286.

Waldschmidt, S. R. 1979. The effect of statistically based models on home range size estimate in Uta stansburiana. Amer. Midl. Nat. 101(1): 236-240.

Wallraff, H. G. 1967. The present status of our knowledge about pigeon homing. Proc. Intl. Ornithol. Congr., 14th, Oxford: 331-358.

Wallraff, H. G. 1982. Matters arising. The homing mechanism of pigeons. Nature 300(5889): 293-294.

Waterman, T. H. 1966. Systems analysis and the visual orientation of animals. Amer. Sci. 54: 15-45.

Waterman, T. H. 1973. Responses to polarized light: animals. In: Biology Data Book, 2nd edition, Vol. II, (P. L. Altman and D. S. Dittmer, eds.), pp. 1272-1289. Fed. Amer. Soc. Exp. Biol., Bethesda, Maryland.

Waterman, T. H. and R. B. Forward, Jr. 1972. Field demonstration of polarotaxis in the fish Zenarchopterus. J. Exp. Zool. 180: 33-54.

Weintraub, J. D. 1968. Winter behavior of the granite spiny lizard, Sceloporus orcutti Stejneger. Copeia 1968: 708-712.

Weintraub, J. 1970. Homing in the lizard Sceloporus orcutti. Anim. Behav. 18: 132-137.

White, J. E. 1964. An index of the range of activity. Amer. Midl. Nat. 71: 369-373.

Wurtman, R. J., J. Axelrod and D. E. Kelly. 1968. The Pineal. Academic Press, New York.

Yeagley, H. L. 1947. A preliminary study of a physical basis of bird navigation. J. Appl. Phys. 18: 1035-1063.

Yeagley, H. L. 1951. A preliminary study of a physical basis of bird navigation. Part II. J. Appl. Phys. 22: 746-760.