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City University of New York PH.D. 1981

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CHEMICAL COMMUNICATION IN THE IGUANID LIZARD *SCELOPORUS JARROVI*

by

KAREN GRAVELLE

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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Abstract

CHEMICAL COMMUNICATION IN THE IGUANID LIZARD
SCELOPORUS JARROVI

by

Karen Gravelle

Adviser: Professor Carol A. Simon

Considerable anecdotal evidence and a few recent quantitative studies suggest that lizards may utilize chemical signals in communicating to conspecifics. This hypothesis was examined in a series of three experiments using an iguanid lizard, *Sceloporus jarrovi*.

In each experiment, resident *S. jarrovi* of different sex/age classes were placed in three out of four similar pens of an outdoor enclosure approximating their natural habitat. The fourth pen was left empty. After residing in these pens for a period of time sufficient to permit them an opportunity to mark these areas with chemical deposits, the residents were removed. Experimental subjects were then individually introduced to the empty enclosure and permitted unrestricted access to all four pens. The responses of the experimental subjects to the four pens were compared to those of control subjects tested prior to the placing of the resident animals in the enclosure. Significant differences

between the experimental and control groups indicated that resident animals had deposited chemicals which were detected and responded to by experimental subjects.

The results indicate that breeding males can detect differences between the chemicals deposited by an adult female, an adult male, and a juvenile male and that they are attracted to an area containing the chemical deposits of the female. The number of tongue extrusions performed by experimental males as compared to controls increased in the pen inhabited by the adult female and decreased in the adult male's pen. Experimental males showed a significant increase over controls in two behaviors, defecating and pelvic rubbing, which could be involved in depositing chemicals, with the increase in pelvic rubs occurring only in the pen housing the adult female.

Breeding males also appeared to be able to discriminate, although with more difficulty, between the deposits of adult and juvenile females and to be attracted to the area containing the deposits of the adult female. The number of tongue extrusions performed by experimental males increased significantly in the adult female's pen but not in the pens housing the juvenile females. Experimental males again performed significantly more pelvic rubs than did controls. However, while an increase occurred in both the pen housing the adult female and

the pen housing the single juvenile female, only the latter was significant.

Adult males tested during non-breeding months showed no differential responses to the chemicals of an adult female, an adult male, and a juvenile male. In contrast to the relatively high rate of pelvic rubbing demonstrated in both experiments conducted during the breeding season, none of the males performed pelvic rubs when not in breeding condition.

Adult females tested in both the breeding and non-breeding seasons showed no significant response to the chemical deposits of conspecifics (an adult female, an adult male, and a juvenile male). In addition, females rarely performed pelvic rubs during either breeding or non-breeding months.

The fact that pelvic rubs were performed only by males in breeding condition suggests that the sexually dimorphic femoral pores present in S. jarrovi may be one source of the chemical signals deposited by males, although substances from the cloacal region could also be deposited by rubbing the pelvis against the substrate. While the response of males to the four pens indicates that adult females deposit chemicals which function in mating, the data shed no light on the source of these chemicals or on how they are deposited.

Finally, there was no evidence that S. jarrovi

respond to the deposits of conspecifics with visual displays.

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CHAPTER I

INTRODUCTION

Any discussion of animal communication should be prefaced by a definition of "communication," particularly since there has been considerable disagreement as to what is meant by the term when it is applied to animals. Smith (1968), Marler (1977), and others have conceptualized the process of communication as a cooperative interaction in which the animal emitting a signal and the animal receiving the signal both benefit from the signal having been sent. In an opposing view, Dawkins and Krebs (1978) emphasize the antagonistic relationship between sender and receiver and define communication in terms of the sender's use of a signal to manipulate the receiver. Although each of these definitions serves a useful heuristic function, the insistence upon viewing communication as either cooperative or exploitative imposes an artificial dichotomy on behavior which may be both mutualistic and manipulative. It seems more parsimonious to define communication as a complex interaction in which signaling may result in benefit to the signaler alone, relatively equal benefit to the signaler and receiver, or unequal benefit to both parties, depending on the situation and the individuals involved. Such a definition obviates the need to label the process in

terms of cooperation or exploitation and directs attention to the contextual functions of the behavior.

The first problem in any study of communication involves determining what constitutes the stimulus, or signal. This task is complicated when signals are transmitted through sensory systems not commonly used in human communication. While we have some intuitive basis for recognizing another species's visual or auditory signals, we are not as able to detect the chemical stimuli produced by another species, much less to recognize these chemicals as signals.

Problems also arise in distinguishing the responses made to a signal. Although communication can certainly take place without an overt response on the part of the receiver, some such response is necessary if we are to determine that a particular signal has been received. Which of the receiver's many behaviors constitute a response to the signal may be difficult to detect, however.

The form any particular signal takes is influenced by a number of factors: 1) the physical possibilities for communication provided by the morphology of the species in question, especially its sensory capacities, 2) the habitat occupied by the species, 3) the function of the signal.

In terms of their sensory systems, lizards have a number of possible avenues for the exchange of signals.

The most obvious of these is vision, a dominant sensory system in non-burrowing saurians (Porter, 1972). The retinas of most diurnal lizards contain typical cones with yellow oil-droplets (Walls, 1942) and, as would be expected in animals having color vision, many of these lizards utilize brightly colored structures (Carpenter, 1978) or color changes (Harris, 1964) in their visual displays. While nocturnal species lack the ability to perceive color, they generally have extremely acute vision even in very poor light (Porter, 1972). The binocular field of lizards is normally 10°-20° and some species, such as the monitor lizards, have a concavity in front of each eye which permits the two visual fields to overlap to approximately 30° (Walls, 1942). The most specialized eyes are found in chameleons. These animals can combine the information from two independently moving eyes, giving them a 360° field of vision (Walls, 1942).

Not all lizards can rely on vision for the transmitting of signals, however. Burrowing species are characterized by degenerate eyes and must find other sensory channels through which to communicate. In addition, nocturnal habitats or densely vegetated areas present limitations for visual communication, forcing even species with adequate vision to rely on other sensory modalities as well. The influence of habitat on saurian communication can be seen in Marcellini's (1977) comparison of

visual and auditory communication in diurnal and nocturnal geckos. Both groups are characterized by excellent vision. Nocturnal geckos, however, produce a multiple-chirp vocalization not present in the repertoire of diurnal species. This vocalization appears to be the functional equivalent of part of the diurnal visual conspecific threat display and it permits communication at distances otherwise impossible in reduced ambient light (Marcellini, 1977).

For most lizards, however, audition is not likely to provide a basis for communication. While all except burrowing species have tympanic membranes (Goodrich, 1958) and can hear air-borne sounds (Wever, 1967), lizards are limited in their capacity to generate them. Only geckos possess vocal chords or other structures used in sound production and thus only these species make noticeable sounds which can be used in communication (Porter, 1972).

Lizards have two chemical senses, olfaction and the vomeronasal tongue-Jacobson's organ system, which might function in communication. These two chemosensory systems are functionally and morphologically separate. Molecules are inhaled into the olfactory system through the nostrils, while in the vomeronasal system, extrusions of the tongue collect molecules from the environment and transfer them to openings in the anterior palate leading to the paired Jacobson's organs. This passageway to the

vomeronasal organs lies below the olfactory passages. The vomeronasal nerve connects the vomeronasal epithelium of the Jacobson's organ to the accessory olfactory bulb, while the olfactory nerve connects the olfactory epithelium of the nasal passages to the main olfactory bulb (Northcutt, 1978). Olfaction appears to be a distance arousal system sensitive to volatiles, while the vomeronasal system seems to function in the close inspection of non-volatiles (Burghardt, 1980; Duvall, 1980; Cowles and Phelan, 1958). A third chemical sense, taste, is present in lizards but is thought to be poorly developed. While there is some controversy concerning the location and number of saurian taste buds (Duvall, personal communication), existing literature states that they are concentrated in the lining of the pharynx with few, if any, on the tongue (Porter, 1972).

In addition to the ability to detect chemicals, lizards also have the capacity to produce chemical deposits which could function as signals. Chemicals exuded in the course of everyday living, such as feces and substances which facilitate the shedding of skin, could convey information about the individual producing them. Potentially more important as sources of chemical signals are the preanal glands, found in the ventral abdominal region just anterior to the cloaca, and the femoral glands, found in the femoral region (Madison, 1977). These glands

function independently of the shedding process and are sensitive to reproductive endocrine cycles (Madison, 1977). The sexually dimorphic femoral glands in particular seem a likely source of chemical signals. In many iguanid males, these glands become enlarged during the breeding season and exude a waxy substance that is apparently rubbed onto the substrate (Cole, 1966). Male Sceloporus also have an apocrine gland anterior to the ventral lip of the cloaca which secretes noticeably during the mating season (Madison, 1977; Burkholder and Tanner, 1974).

Very little is known about the tactile senses in reptiles, although Miller and Kasahara (1967) state that the skin of lizards is innervated by the same basic types of nerve endings that are found in the skin of mammals. In nocturnal species such as geckos, tactile interactions play an important part in courtship. The male Coleonyx variegatus pokes the female with his nose, grabs her in his jaws and pushes her in front of him in a ritualized strut (Oliver, 1955). In diurnal lizards, however, physical contact between male and female generally does not occur until mating has actually begun.

Thus, the major sensory pathways available to most lizards for the exchange of signals are visual and/or chemical. However, functional limitations inherent in visual communication may result in the evolution of a

chemically based system even in those species not restricted by morphology or habitat in their use of visual displays. Communication through visual, auditory or tactile senses requires both sender and receiver to be present in the same space (as defined by the visual, auditory or tactile range of the species) and at the same time. As Auffenberg (1977) points out, chemical signals are the only ones useful in a future context. Considering that many lizards are territorial, selection pressure might be expected to operate in favor of the development of a means of territorial maintenance which does not require the constant presence of the resident animal. Many mammalian species accomplish this by marking their territories with scent. While territorial marking has not yet been demonstrated for any reptile (Burghardt, 1970), it would be reasonable to expect the use of chemical communication in lizards which have both olfactory and vomeronasal organs.

Of the two chemosensory systems, both theoretical and practical considerations point to the vomeronasal as the more appropriate focus for the study of saurian chemical communication, particularly in a field setting. Recent work on the olfactory and vomeronasal systems in such diverse groups as snakes and hamsters indicates that input from the vomeronasal system is more important than input from the olfactory system in mediating mating

(Kubie et al, 1978; Powers and Winans, 1975).

On a practical level, it is difficult to determine conclusively whether a lizard is smelling merely by observing its behavior. Extrusions of the tongue, however, can provide a discrete, unambiguous measure of the animal's use of the vomeronasal system. Moreover, observations of tongue extrusions can be made through binoculars at some distance from the animal, thus further reducing interference in its behavior. Therefore, while the two chemical systems probably interact to some degree (see Conclusions), the vomeronasal is both more accessible and likely to be more directly involved in social behavior and, hence, will be the focus of this study.

A review of the literature suggests that different lizard species rely on the vomeronasal system to varying degrees. Some indication of the differing importance of this chemical system is suggested by Bissinger and Simon's (1979) finding of a correlation between the number of tongue extrusions performed, the degree of Jacobson's organ development, and the degree of tongue bifurcation in six families of lizards. Similarly, Gove (1975; 1979) compared seven families of lizards and found a parallel relationship between snake-like condition of the tongue, extension of the tongue relative to snout length, and area sampled by the tongue (see Burghardt, 1977).

While these studies point to differing degrees of

dependence on the vomeronasal system across species, the functions the system serves for each group remain unclear. A number of descriptive studies have implicated the vomeronasal system in a wide variety of saurian social interactions. Tongue-extruding has been mentioned in connection with hatchling aggregation (Burghardt et al, 1977), chuckwalla dominance (Berry, 1974), skink maternal behavior (Noble and Kumpf, 1936; Evans, 1959), spacing in monitor (Auffenberg, 1978) and iguanid (Gravelle and Simon, 1980) lizards, and the courtship behavior of a number of species including Uta stansburiana (Tinkle, 1967), Sceloporus in the torquatus group (Hunsaker, 1962), chuckwallas (Berry, 1974) and the nocturnal gecko, Coleonyx variegatus (Greenberg, 1943).

Recent experimental work has begun to provide quantitative data indicating that at least some lizards utilize chemicals in communicating to conspecifics. In both field experiments (Simon et al, 1981) and in laboratory studies (De Fazio et al, 1977), adults of the iguanid species, Sceloporus jarrovi, extruded the tongue significantly more often in novel environments than in home areas. Since Simon's study clearly showed that this species does not use the vomeronasal system in foraging, a probable function of the system in these situations is in mediating interactions between conspecifics. In a study using juveniles (Bissinger and Simon, 1981), S. jarrovi respond-

ed to unfamiliar areas previously inhabited by juvenile conspecifics with significantly more tongue extrusions than to unfamiliar clean areas, which in turn elicited significantly more extrusions than the home cage, thus suggesting that S. jarrovi respond to the chemicals of other lizards.

Further support for the hypothesis that these iguanids might be communicating chemically comes from work done with a closely related species, Sceloporus occidentalis. In a laboratory study (Duvall, 1979), males licked bricks covered with chemical deposits left by other male conspecifics significantly more often than they licked unmarked bricks. While males did not show increased licking in response to female-labeled bricks and while females did not differentiate in terms of licking between bricks marked by either sex and unlabeled bricks, both sexes performed push-up displays after licking marked bricks. This behavior never occurred in response to unmarked bricks.

Other laboratory evidence points to the use of conspecific signals in non-iguanid groups as well. In experiments done with skinks, Duvall et al (1980) found that five-line skinks in post-breeding condition significantly approached the odors of same-sex conspecifics while responding randomly to the odors of opposite-sex conspecifics. Ground skinks, on the other hand, significantly

avoided the odors of male conspecifics while males, but not females, significantly approached female odors. Neither species responded to odors of the other. This study, however, did not differentiate between the use of olfaction and the vomeronasal system.

In determining which species would be most appropriate for the study presented here, a number of factors were taken into consideration. Although nocturnal and/or burrowing species were likely to utilize the vomeronasal system to the greatest degree, this heavy reliance on the system to serve multiple functions presented serious drawbacks for a study of chemical communication. Since these species appeared to use the vomeronasal system in many aspects of their lives, determining when the system was being used in communication would be difficult and time consuming. In addition, species which rely heavily on chemical senses often extrude and retract the tongue at speeds too fast for accurate counting. Finally, as this study was to be carried out in a natural setting with a minimum of interference in the subjects' normal activities, the animal chosen had to be easily observable from a distance. A diurnal, non-burrowing species which did not rely extensively on chemical sensory systems seemed most likely to satisfy these requirements. Moreover, a considerable portion of the research in saurian communication discussed above involved these species and provided

evidence that Sceloporus lizards in particular might communicate chemically.

Several Sceloporus species are indigenous to the area surrounding the Southwestern Research Station of the American Museum of Natural History in Portal, Arizona. Of these, Sceloporus jarrovi, a diurnal lizard which perches on exposed surfaces, is easily visible, is relatively undisturbed by the presence of people, and extrudes the tongue at a rate compatible with accurate quantification. In addition, extensive field observations have conclusively shown that this species does not use the vomeronasal organ in foraging (Simon et al, 1981). The elimination of foraging as a possible use of the vomeronasal system provides a tremendous advantage in detecting the system's use in social interactions. For a number of reasons, therefore, S. jarrovi was chosen for this study.

Having decided upon the appropriate chemosensory system and species for use in the study, the only remaining issues were the two problems raised at the beginning of the paper: 1) How does one determine that a chemical functions as a signal? 2) How does one determine which behaviors indicate that another individual has received this signal?

Since it would have been extremely difficult to determine which of many body substances might serve as

signals and to obtain sufficient quantities of these chemicals for a field experiment, this study focused not on identifying the actual chemical signals but merely on trying to demonstrate that they were present. Behaviors which indicated that subjects detected the chemical deposits of conspecifics and modified their behavior in response to these chemicals were considered evidence that chemical signals were present.

In the case of S. jarrovi, several behaviors seemed reasonable indications that an animal might be detecting and responding to a chemical signal: 1) Since tongue extrusions are a clear indication of the use of the vomeronasal system, changes in the number of extrusions and/or rate of extruding should indicate when and where chemicals were being detected. 2) A common response to the detection of a signal is to send a return signal. Thus, an increase in signaling behavior, either in terms of visual displaying or in behaviors which might function in the depositing of chemicals (defecating, rubbing part of the body against the substrate, etc.) could suggest that the subject was responding to a signal. 3) Finally, since many signals function in either attracting or repelling conspecifics, the amount of time an individual spent in various areas could indicate the presence of chemical signals there.

In the following series of experiments, a common

design was utilized to determine the presence of chemical signals. Resident *S. jarrovi* representing specific sex/age classes were placed in three out of four similar compartments (or pens) of an outdoor enclosure approximating their natural habitat. After residing in these pens for a period of time sufficient to permit them an opportunity to mark the areas with chemical deposits, the resident animals were removed. Experimental subjects were then individually introduced to the empty enclosure and permitted unrestricted access to all four pens.

The three response categories outlined above were considered reasonable indicators that a signal might have been received. The responses made to the four pens by experimental subjects were compared to those made by control subjects tested in the enclosure prior to the placing of resident animals in the pens. Significant differences in the responses of the two groups to the four pens indicated that resident animals had deposited chemicals which were detected and responded to by experimental subjects.

In Experiment 1, adult males and adult females were tested during the breeding season to determine (a) if they could detect chemicals deposited by conspecifics (an adult male, an adult female, and a juvenile male) and (b) if so, whether they could determine the sex and maturity of the depositor.

In Experiment 2, adult males and adult females were tested during non-breeding months to determine (a) if they could detect chemicals deposited by conspecifics (an adult male, an adult female, and a juvenile male) and (b) if so, whether they could determine the sex and the maturity of the depositor.

In Experiment 3, adult males were tested during the breeding season to see if they could distinguish between the chemical deposits of adult and juvenile females.

CHAPTER II

GENERAL METHODS AND MATERIALS

Subjects

The animals used in this series of experiments, Sceloporus jarrovi, are insectivorous lizards occurring in elevated areas of Mexico, southern New Mexico, and southern Arizona.

During the months in which they are active (May - October), S. jarrovi maintain exclusive territories against same-sex adults and against all juveniles and, where space is available, juveniles defend territories against all other juveniles. Under usual densities, only adult male and female territories overlap both temporally and spatially, presumably to facilitate mating (Simon, 1976; Simon and Middendorf, 1976). Male aggression, activity, and territory size increase as the breeding season approaches and males shift their territories to respond to the location of females (Ruby, 1976). Females, on the other hand, generally establish permanent territories in May and female aggression and activity drop in the fall (Ruby, 1976). Territories are maintained at least in part with the use of visual displays involving push-ups, gular extensions, lateral flattening of the body, etc.

S. jarrovi are ovoviviparous and mate in September and October (Goldberg, 1971). Males range further than

females and mate polygamously, while females generally mate only once (Ruby, 1976). Like territorial behavior, mating is at least partially mediated by visual communication (Ruby, 1977). Young are born in the spring at lower altitudes and in the summer at higher altitudes. Of the females born in the spring at lower elevations, 60% of the survivors will reach maturity by the following fall breeding season (Ballinger, 1973).

Thirty control and 30 experimental adult S. jarrovi (snout-vent length $\geq$ 6.0 cm) served as subjects in each experiment. Animals were captured anywhere from immediately prior to testing up to two days before testing. In the interim between capture and testing, they were maintained outdoors in separate glass terraria, usually within visual range of other waiting subjects.

Apparatus

A large square enclosure (8 X 8 m) was constructed outdoors in typical S. jarrovi habitat. The ground within the enclosure was divided by narrow, shallow trenches dug diagonally from corner to corner. Two portable board dividers joined in an 'X' were designed to fit into the diagonal trenches, thereby dividing the enclosure into four equally-sized triangular pens. The distribution of sun, shade, and rock perches was similar in the four areas.

A small movable wooden platform, 15 cm square and 60 cm high, served as a release stand for the subject

being tested.

Procedure

Control. Prior to placing the resident animals in their home pens, the 30 control subjects were individually tested to determine baseline performances in each of the four areas.

The board dividers were removed, leaving only the ground area marked by shallow trenches. The release stand (freshly washed with water for each subject) was set in the center of the enclosure and the lizard was placed on top. The animal was permitted to remain on the stand until it jumped into the enclosure voluntarily. This jump signaled the beginning of a 30-minute observation period. Observations were made through binoculars from outside the enclosure. No more than three control subjects were tested per day.

The animals typically responded to being handled in one of two ways, either by 'freezing' or by running away from the experimenter. The release stand was designed to eliminate problems caused by these responses. If carefully placed on the stand, the subject would remain there until the experimenter could get out of the enclosure. Since there was no limit on the time the subject could remain on the stand, it could 'unfreeze' at its own pace while any droppings made during this period could not contaminate the ground area.

With the exception of the control condition of Experiment 1, the direction in which the subject faced when placed on the stand and the direction from which I left the enclosure were balanced evenly among the four pens for both males and females.

The following behaviors were recorded for each subject:

1) The number of tongue extrusions performed in each pen.
2) The time spent in each pen.
3) The number of potential marking behaviors performed in each pen.

   As several behaviors - defecations, pelvic rubs (rubbing the pelvic area against the substrate), and chin wipes (wiping the chin/face against the substrate) - were possibly involved in the depositing of chemicals, data were collected on each separately.
4) The number of seconds spent bobbing (engaging in push-up displays) in each pen and the number of seconds spent bobbing while extruding the tongue in each pen.
5) The number of pens entered.
6) Which pen the subject entered first.

Experimental. Following completion of control testing, the board dividers were placed in the enclosure, forming four separate pens. Resident S. jarrovi representing specific sex/age classes were placed in three out of the four pens. Resident lizards were allowed to inhabit

their pens for 5-6 days before any testing of experimental subjects was undertaken so that the residents would have an opportunity to deposit chemicals throughout their home areas. Testing was done every third day both to reduce disturbance to the residents and to permit them ample opportunity to freshly mark their home areas.

On each test day, the resident lizards and the dividing boards were removed, leaving only the ground area separated by shallow trenches. Each experimental subject was placed on the release stand at the center of the enclosure and observed for a 30-minute period beginning when the animal jumped off the stand into the enclosure. The direction in which the subject faced when placed on the stand and the direction from which I left the enclosure were balanced evenly among the four pens for both males and females. Data were recorded as described above. In order to reduce the possibility that chemical deposits from the resident lizards might become overpowered by those left by experimental subjects, only three subjects were tested on each test day.

The study was conducted at the Southwestern Research Station of the American Museum of Natural History located in the Chiricahua Mountains near Portal, Arizona. This area (1,646 meters) is at the lower range of altitudes inhabited by S. jarrovi.

CHAPTER III

EXPERIMENT 1

If chemicals are used by Sceloporus jarrovi in communicating with conspecifics, two areas in which these chemical signals might function are in the maintenance of territories and/or in mating.

S. jarrovi of both sexes are generally territorial throughout the active period of May-October. If chemical cues are involved in territorial behavior, both male and female adults traveling outside their own territories might be expected to avoid an area containing the chemical deposits of another adult of the same sex.

If chemicals serve to mediate mating, we might expect breeding adults to be attracted to areas containing the deposits of an adult of the opposite sex. However, as breeding males range in search of females and mate polygamously, while females generally remain in established territories and mate only once per season, we might expect the attraction of males to areas containing female deposits to be stronger than the attraction of females to areas containing male deposits.

The following experiment was designed to investigate these hypotheses.

Methods

Subjects

Fifteen male and 15 female adult S. jarrovi served

as control subjects. Since control subjects were tested in August prior to the breeding season, presumably none had mated during the current year. Fifteen male and 15 female adult experimental subjects were tested during the breeding months of September and October. These animals may have mated prior to testing. Due to the limited availability of lizards, three control males and six control females also served as experimental subjects, but no subject served more than once per condition.

Procedure

Control. During the last two weeks of August (8/19-8/31) 1978, prior to placing the resident animals in the enclosure, the 30 control subjects were tested to establish baseline data for the four pens.

Unfortunately, a problem concerning the release procedure arose while these subjects were being tested. Since the time period between release and the subject's jump from the stand into the enclosure was typically a long one - 15 minutes to almost two hours - and since subjects repositioned themselves frequently during this period, I assumed they were not influenced by the direction in which they were originally facing when placed on the stand or by the direction from which I left the enclosure. However, during testing of these subjects, it appeared that, in spite of the use of the stand, these factors might have an effect on which pen subjects entered first. At this

point, I was able to balance these two factors for the control group as a whole but not for males and females separately (see Table 1).

Experimental. Following completion of control testing, the board dividers were placed in the enclosure, forming four separate pens. Three of these pens were established as the home for a single resident S. jarrovi. Pen 1 was inhabited by an adult female (snout-vent length 7.3 cm), Pen 2 by an adult male (s-v length 7.4 cm), and Pen 3 by a juvenile/sexually immature male (s-v length 4.8 cm). Pen 4 was left empty (see Figure 1).

Although the four areas of the enclosure appeared similar to me, there was evidence that control males did not perceive them as such (see Results). If chemical cues were being used during the breeding season, they could be expected to function in repelling same-sex adults and/or attracting opposite-sex adults. Therefore, the adult male resident was placed in the pen which seemed most preferred by control males (Pen 2), while the female resident was placed in the pen males preferred least (Pen 1). Female control subjects demonstrated no particular pen preferences.

Resident lizards were allowed to inhabit their pens for 5-6 days before any testing of experimental subjects was undertaken.

The 30 experimental animals were tested during a

Table 1. Experiment 1: Control and Experimental Release Procedures.

	Control Release Procedure		Experimental Release Procedure	
	Observer Exited	Subject Facing	Observer Exited	Subject Facing
MALES				
Pen 1	4	3	4	4
Pen 2	4	3	3	4
Pen 3	2	5	4	4
Pen 4	5	4	4	3
FEMALES				
Pen 1	5	5	4	3
Pen 2	3	4	4	4
Pen 3	5	2	3	4
Pen 4	2	4	4	4
TOTAL SUBJECTS				
Pen 1	9	8	8	7
Pen 2	7	7	7	8
Pen 3	7	7	7	8
Pen 4	7	8	8	7

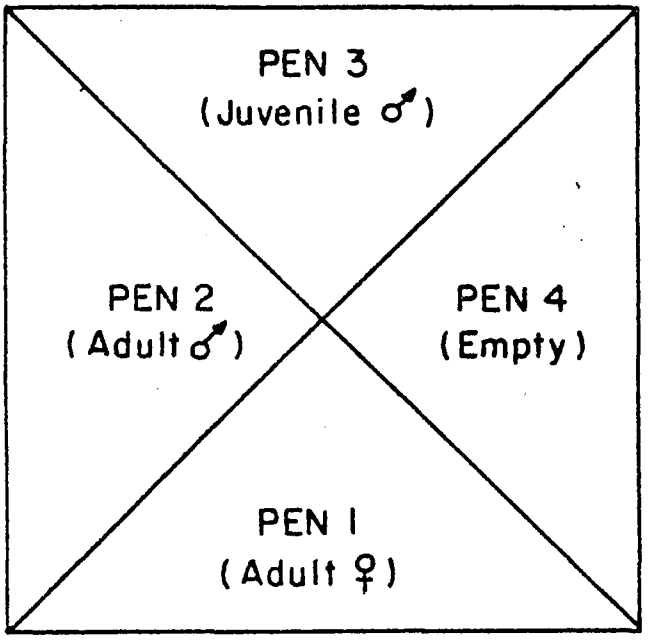

Figure 1. Experiments 1 and 2: Placement of the Resident Animals in the Four Pens.

five week period in the breeding months of September and October (9/9-10/13) 1978.

Results

Possible Effects of Subject Chemical Deposits

Before presenting data on subject responses to resident chemical cues, it is important to illustrate that these behaviors were not instead responses to the chemicals left by previous subjects.

In order to examine the possible effects of subject chemical deposits on subsequent subjects, I calculated (1) the number of tongue extrusions performed by each subject in the pens which the immediately preceeding subject had entered, and (2) the overlap in minutes between the time a subject spent in each of the four pens and the time spent in each of these pens by the immediately preceeding subject.

Experimental subjects were divided into two categories: Long Delay Group. For the first experimental subject of each test day, the immediately preceeding subject was the last subject of the previous test day. As testing was done every third day, these two subjects were separated by a two-day period during which the resident animals had full access to the enclosure. Short Delay Group. For both the second and third subjects of each test day, the immediately preceeding subject was an animal which had been tested 45 minutes to a few hours earlier.

If chemicals deposited by subjects were either attracting or repelling subsequent subjects, either (1) the mean tongue extrusions demonstrated by the Long Delay Group should in some way differ from that of the Short Delay Group, and/or (2) the mean overlap time of the Long Delay Group should differ in some respect from that of the Short Delay Group.

Control data were also analyzed in this manner. For control subjects in the Long Delay Group, however, the time period between the first subject of each test day and the last subject of the previous test day was much shorter (overnight) than the time period for experimental subjects in the Long Delay Group (two days and two nights).

In the case of both experimental males and experimental females, there were no significant differences between the Long Delay and Short Delay Groups in terms of either mean number of tongue extrusions (Males: $t(13)=0.97$, ns; Females: $t(12)=1.33$, ns) or in terms of mean overlap time (Males: $t(13)=1.14$, ns; Females: $t(12)=0.04$, ns). In addition, for both experimental males and experimental females, there were no significant differences as a function of the sex of the immediately preceeding subject in terms of either mean number of tongue extrusions (Males: $t(13)=0.19$, ns; Females: $t(12)=0.09$, ns) or mean overlap time (Males: $t(13)=0.07$, ns; Females: $t(12)=0.11$, ns).

When control data were analyzed in this manner, there

were again no significant differences, either for males or females, between the mean number of tongue extrusions performed by the Long Delay and Short Delay Groups (Males: $t(13)=1.56$, ns; Females: $t(13)=0.77$, ns) or between the mean overlap times of the Long Delay and Short Delay Groups (Males: $t(13)=1.48$, ns; Females: $t(13)=0.07$, ns). In addition, for both control males and control females, there were no significant differences as a function of the sex of the immediately preceeding subject in terms of either mean number of tongue extrusions (Males: $t(13)=0.25$, ns; Females: $t(13)=0.29$, ns) or mean overlap time (Males: $t(13)=1.26$, ns; Females: $t(13)=0.95$, ns).

Thus, from all indications, it does not seem that either the number of tongue extrusions a subject performed in a pen or the time it spent in any particular area was significantly influenced by chemicals which might have been deposited by the immediately preceeding subject.

Responses to Resident Chemical Deposits

Control Data

Observations of control subjects indicated that males may have preferred one pen over the other three. Since the control condition of Experiment 1 was the only condition in which the direction subjects faced when placed on the stand and the direction from which I exited after releasing them were not balanced evenly across the four pens, the control data for this experiment were analyzed

separately.

Males. A one-way ANOVA ($F(3,56)=3.78$, $P<0.05$) followed by a Student-Newman-Keuls (SNK) test showed that significantly more tongue extrusions ($P<0.05$) were performed in Pen 2 than in any of the other three pens (see Table 2). The remaining areas, on the other hand, showed no significant cross-pen differences in number of tongue extrusions. The four pens also differed in terms of bobbing seconds associated with tongue extrusions ($F(3,56)=3.68$, $P<0.05$). Again, significantly more bobbing with tongue extrusions occurred in Pen 2 ($P<0.05$, SNK test) (see Table 2). Finally, eight of the 15 control males entered Pen 2 first.

No preference was found in terms of the other behaviors measured. There were no significant differences in the time spent in each pen ($F(3,56)=0.90$, ns) in the rates (number of tongue extrusions/minutes spent in pen) of extruding in each of the four areas ($F(3,56)=0.40$, ns), nor in the total number of seconds spent bobbing in each pen ($F(3,56)=2.35$, ns). Only one possible instance of marking (a chin wipe) occurred.

As mentioned earlier, these data were influential in determining the placing of resident animals in their home pens.

Females. Female control subjects appeared to find no differences between the four pens: the numbers of tongue extrusions did not differ from pen to pen ($F(3,56)=$

Table 2. Mean Number of Tongue Extrusions and Mean Seconds Spent Bobbing in Association with Tongue Extrusions Performed by Control Males in Each of the Four Pens. Experiment 1.

	PEN 1	PEN 2	PEN 3	PEN 4
TONGUE EXTRUSIONS				
Control (n=15)	1.5 ± 2.3	6.1 ± 8.2	2.1 ± 4.1	0.8 ± 1.1
BOBBING WITH TONGUE EXTRUSIONS				
Control (n=15)	0.0 ± 0.0	2.5 ± 4.5	0.7 ± 1.2	0.1 ± 0.3

0.86, ns); the rates of tongue extruding showed no significant cross-pen differences ($F(3,56)=0.94$, ns); there were no significant differences in the time spent in each pen ($F(3,56)=0.12$, ns); the total seconds spent bobbing did not differ across pens ($F(3,56)=0.63$, ns); there were no significant differences in the bobbing seconds per pen associated with tongue extruding ($F(3,56)=0.54$, ns); and females showed no particular preference in terms of the first pen entered. Only two possible markings (both chin wipes) were demonstrated.

Comparison of Control vs. Experimental Conditions

Males.

Time spent in each pen. If chemicals deposited by conspecifics during the breeding season influence the social behavior of S. jarrovi, we would expect experimental males to spend more time than controls in an area containing chemicals left by an adult female and less time than controls in an area containing chemicals left by another male.

A two-way ANOVA of the time spent in each pen (pen X condition) showed no significant main effects (Pen: $F(3,112)=0.54$, ns; Condition: $F(1,112)=0.00$, ns) and no significant interaction between pen and condition ($F(3,112)=0.38$, ns). However, as Table 3 illustrates, there were differences in the amount of time control and experimental males allotted to each of the four pens, and these differences

Table 3. Mean Time Spent and Mean Tongue Extrusions Performed in Each of the Four Pens. Males, Experiment 1.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TIME (MIN)				
Control (n=15)	4.8 ± 8.1	10.4 ± 12.0	8.8 ± 11.9	6.0 ± 9.1
Experimental (n=15)	7.6 ± 10.9	8.4 ± 10.9	6.7 ± 10.6	7.2 ± 11.4
TONGUE EXTRUSIONS				
Control (n=15)	1.5 ± 2.3	6.1 ± 8.2	2.1 ± 4.1	0.8 ± 1.1
Experimental (n=15)	8.6 ± 16.3	1.9 ± 2.7	4.4 ± 7.2	1.9 ± 2.9

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

were compatible with the above hypothesis. Compared to controls, experimental males spent more time in the female's home area and less time in both the pens inhabited by males. They also spent more time in the pen which remained empty than did controls.

Number of tongue extrusions. As Table 3 illustrates, control and experimental subjects showed several differences in terms of tongue extrusions. Experimental males performed more tongue extrusions than did controls, although this increase was not significant ($F(1,112)=1.38$, ns). The two groups differed markedly in the distribution of extrusions among the four pens, as seen in the significant interaction between pen and condition ($F(3,112)=3.09$, $P<0.05$). This interaction appears to have resulted from the increase in extrusions performed by experimental males in the adult female's pen and the decrease in extrusions made by them in the adult male's pen. There was no significant pen effect ($F(3,112)=1.37$, ns).

Rate of extruding. As the number of tongue extrusions in an area could conceivably be a function of the time spent in that area, the tongue extrusion data were also analyzed in terms of the rate of extruding in each of the four pens. The rate data, however, were calculated differently from the data concerning other behavioral categories. For all data except rates, subjects were considered to have performed zero behaviors in those pens they did

not enter and, thus, each subject received scores for all four pens. However, since subjects cannot be said to have zero rates of performance in pens they never entered, the mean rate of extruding for subjects in that treatment condition was substituted for the missing scores. This had the effect of artificially reducing both the inter-subject variability and the inter-pen differences. In addition, since each subject entered, on the average, only two out of the four pens (see below), approximately half of the raw data used in the following statistical analyses consisted of the substituted group means. Thus, results based on these rate calculations should be interpreted cautiously.

Experimental males extruded the tongue at a significantly higher rate than did controls ($F(1,112)=5.78$, $P<0.05$), but this increase did not occur evenly across pens. Compared to controls, the rate at which experimental males extruded the tongue rose in the adult female's home area and in the pen inhabited by the juvenile male, dropped in the adult male's pen, and showed little change in the empty pen (see Table 4). This interaction between pen and condition was significant ($F(3,112)=3.32$, $P<0.05$) and was due to the increased rates of extruding in the adult female's pen ($F(1,28)=5.11$, $P<0.05$) and in the juvenile male's area ($F(1,28)=13.50$, $P<0.01$). Shifts in the rates of extruding in the adult male's pen ($F(1,28)=2.00$, ns) and in the empty

Table 4. Mean Number of Tongue Extrusions Performed Per Minute in Each of the Four Pens. Males, Experiment 1.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
Control (n=15)	.37 ± .17	.45 ± .20	.34 ± .20	.38 ± .46
Experimental (n=15)	.72 ± .58	.33 ± .25	.61 ± .21	.43 ± .21

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

pen ($F(1,28)=0.15$, ns) were not significant. There was no significant pen effect ($F(3,112)=1.47$, ns).

Marking. As seen in Table 5, experimental males showed a clear increase over control males in the behaviors which could be involved in depositing chemicals. Moreover, the increase in these behaviors occurred only in the pen housing the adult female.

Both the difference between the number of experimental and control markings and the interaction between pen and condition were significant (Pen: $F(3,112)=2.49$, ns; Condition: $F(1,112)=5.32$, $P<0.05$; Interaction: $F(3,112)=2.80$, $P<0.05$). Not only were there significantly more marking attempts by experimental than control males, but the number of individuals performing them also differed significantly. While only one of the 15 control males marked, seven of the 15 experimental males demonstrated some marking behavior (Fisher Exact Probability Test, $P<0.025$).

When each of the three marking categories are examined separately, it appears that they were not of equal importance. While no control males defecated or rubbed the pelvic area against the substrate, five of the 15 experimental males defecated and six pelvic rubbed. The increase in subjects demonstrating these behaviors was significant in both cases (Defecations: $P<0.025$; Pelvic rubs: $P<0.01$). There was no difference between the number of experimental

Table 5. Total Marking Behaviors Performed in Each of the Four Pens: Defecations (DEF), Pelvic Rubs (PR), and Chin Wipes (CW). Males, Experiment 1.

	Pen 1 (Adult Female Pen)			Pen 2 (Adult Male Pen)			Pen 3 (Juvenile Male Pen)			Pen 4 (Empty Pen)		
	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW
Control (n=15)	0	0	0	0	0	1	0	0	0	0	0	0
Experimental (n=15)	2	10	3	1	0	0	1	1	0	1	1	0

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

(1) and control (1) males performing chin wipes, however.

The total number of defecations performed rose significantly from none in the control condition to five in the experimental condition ($t(28)=2.65$, $P<0.05$). Control males performed no pelvic rubs compared to a total of 12 performed by experimental males ($t(28)=1.98$, $P<0.10$). Chin wipes, in contrast, rose only slightly from one in the control condition to three in the experimental condition ($t(28)=0.63$, ns).

Seconds spent bobbing. A two-way ANOVA of the seconds spent bobbing showed no significant main effects (Pen: $F(3,112)=2.12$, ns; Condition: $F(1,112)=0.01$, ns) and no significant interaction between pen and condition ($F(3,112)=1.68$, ns) (see Table 6).

More important, there were no significant differences between control and experimental males in terms of bobbing done in conjunction with tongue extrusions (Pen: $F(3,112)=2.24$, ns; Condition: $F(1,112)=0.00$, ns; Interaction: $F(3,112)=2.29$, ns).

While control and experimental males differed in the number of tongue extrusions performed, the two groups showed virtually the same mean number of seconds spent bobbing associated with tongue extruding (see Table 7).

Number of pens entered. Control males entered a mean number of 1.8 pens, while experimental males entered a mean of 1.9 pens ($t(28)=0.26$, ns). No animal in

Table 6. Mean Total Seconds Spent Bobbing and Mean Seconds Bobbing in Association with Tongue Extrusions in Each of the Four Pens.
Males, Experiment 1.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TOTAL BOBBING				
Control (n=15)	0.9 ± 2.1	7.9 ± 15.5	3.4 ± 7.2	0.5 ± 1.4
Experimental (n=15)	4.0 ± 7.1	2.9 ± 4.7	4.0 ± 7.0	1.2 ± 2.4
BOBBING WITH TONGUE EXTRUSIONS				
Control (n=15)	0.0 ± 0.0	2.5 ± 4.5	0.7 ± 1.2	0.1 ± 0.3
Experimental (n=15)	0.7 ± 1.3	0.7 ± 2.1	1.2 ± 2.5	0.6 ± 1.8

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Table 7. Mean Seconds Spent Bobbing and Mean Seconds Bobbing In Association With Tongue Extrusions. Males, Experiment 1.

	Seconds Spent Bobbing	Seconds Bobbing In Association With Tongue Extrusions
Control (n=15)	12.7 ± 15.4	3.2 ± 4.4
Experimental (n=15)	12.1 ± 10.3	3.1 ± 3.7

either group entered all four pens.

Pen entered first. As mentioned earlier, eight of the 15 control males jumped off the stand and into Pen 2 first (see Table 8). Since two procedures followed in the releasing of subjects (ie. the direction a subject was facing when placed on the stand and the direction from which I left the enclosure) were not evenly balanced across pens, the data were examined to determine whether these procedures influenced which pen a subject entered first.

As Table 9 shows, there was a clear tendency for a subject to enter first the pen which he was facing when placed on the stand and not to enter first the pen directly behind him. An even stronger tendency was not to enter first the pen from which the observer exited and to enter first the pen directly opposite the observer's exit route.

However, these two tendencies did not apply equally to all four pens. Control males always entered Pen 2 first when released facing this pen and always entered Pen 2 first when the observer exited from the opposite pen. At the other extreme, male control subjects never entered Pen 1 first when released facing this pen and never entered Pen 1 first when the observer exited from the opposite pen. Subjects entered Pens 3 and 4 first approximately half the times when they were released facing the pen in question and half the times when the

Table 8. Release Procedure and Initial Pen Preference. Males, Experiment 1.

	Release Procedure		First Pen Entered
	Observer Exited	Subject Facing	Number of Subjects Entering Pen First
Control			
Pen 1	4	3	1
Pen 2	4	3	8
Pen 3	2	5	3
Pen 4	5	4	3
Experimental			
Pen 1	4	4	1
Pen 2	3	4	5
Pen 3	4	4	3
Pen 4	4	3	6

Table 9. Factors Associated with Choice of First Pen Entered. Males, Experiment 1.

SUBJECT ENTERED	CONTROL	EXPERIMENTAL
Pen Facing	7	8
Pen Opposite Pen Facing	0	1
Pen on Either Side of Pen Facing	8	6
****		
Pen From Which Observer Exited	0	0
Pen Opposite Observer's Exit Route	9	11
Pen on Either Side of Observer's Exit Route	6	4

observer exited from the opposite pen.

Theoretically, combining these two factors (ie. releasing a subject facing a particular pen with the observer exiting from the opposite pen) should have further enhanced the probability that a subject would enter a particular pen. However, not only was this combination balanced among the four pens but even combining these two factors did not induce subjects to enter Pen 1 first, while the combination always resulted in subjects entering Pen 2 first. Subjects entered Pens 3 and 4 first half the times that this particular combination occurred.

Thus, the data indicate that control males entered Pen 2 first more frequently than they did the other three pens not because of procedural problems in releasing the subjects but because of some factor(s) involving Pen 2.

Experimental males entered Pens 4 and 2 first (six and five times, respectively) more frequently than they entered Pens 1 and 3 first (once and three times, respectively). The fact that the release procedures in question were balanced for experimental subjects meant, of course, that they differed in this respect from the control procedures. Therefore, the experimental data were also analyzed to determine if subjects showed an initial preference similar to that of controls for Pen 2.

As Table 9 illustrates, experimental males, like controls, showed a clear tendency to enter first the pen they

were facing when placed on the stand and not to enter first the pen directly behind them. Like controls, experimental males showed an even stronger tendency not to enter first the pen from which the observer exited and to enter first the pen directly opposite the observer's exit route.

As in the case of control males, experimental males did not demonstrate these tendencies equally across the four pens. Even more important, control and experimental results tended to mirror each other in this respect. Experimental males entered Pen 2 first two out of the three times they were released facing this pen and always entered Pen 2 first when the observer exited from the opposite pen. In addition, in the one instance in which an experimental subject entered first the pen directly behind him, this pen was Pen 2. At the other extreme, male experimental subjects rarely entered Pen 1 first when released facing this pen and never entered Pen 1 first when the observer exited from the opposite pen. Subjects entered Pen 3 first half the times that they were released facing this pen and three out of four times that the observer exited from the opposite pen. Control and experimental responses to Pen 4 differed, however, in that experimental males seemed more likely to enter this area first than did controls.

As in ths case of control males, the instances in

which a subject was released facing a particular pen with the observer exiting from the opposite pen were balanced among the four pens. This combination always resulted in subjects entering Pens 2, 3, and 4 first but it was not as successful in inducing them to enter Pen 1 first.

Intra-group comparisons. Because of indications that males may have preferred Pen 2, subjects in the first half of each condition were compared with subjects in the second half of each condition in terms of the number of tongue extrusions performed and the time spent per pen to determine if the two halves responded in a similar manner to the four pens.

A two-way ANOVA showed no significant differences in the number of tongue extrusions performed by the two control groups ($F(1,52)=0.00$, ns) and no significant interaction between group and pen ($F(3,52)=0.81$, ns). There was, however, a significant pen effect ($F(3,52)=3.47$, $P<0.05$), with Pen 2 receiving significantly more extrusions ($P<0.05$). A two-way ANOVA of the time spent by the two control groups in each of the four pens showed no significant main effects (Pen: $F(3,52)=0.78$, ns; Group: $F(1,52)=0.00$, ns) and no significant interaction ($F(3,52)=0.66$, ns).

A two-way ANOVA showed no significant difference in the number of tongue extrusions performed by the two experimental groups ($F(1,52)=0.82$, ns) and no significant interaction between group and pen ($F(3,52)=0.71$, ns).

Unlike control results, analysis of the tongue extrusions performed by experimental males showed no significant pen effect ($F(3,52)=1.57$, ns). A two-way ANOVA of the time spent by the two experimental groups in each of the four pens showed no significant main effects (Pen: $F(3,52)=0.08$, ns; Group: $F(1,52)=0.00$, ns) and no significant interaction ($F(3,52)=0.77$, ns).

Females.

Time spent in each pen. If S. jarrovi respond to chemicals deposited by conspecifics during the breeding season, we would expect experimental females to spend less time than controls in an area containing chemicals left by another adult female. We would not expect females to be as attracted as males to areas containing chemicals deposited by adults of the opposite sex, however, since females of this species do not range in search of mates.

As in the case of males, no significant differences between control and experimental females were found in terms of the time spent in each of the four pens (Pen: $F(3,112)=1.21$, ns; Condition: $F(1,112)=0.00$, ns; Interaction: $F(3,112)=1.12$, ns). However, as seen in Table 10, there were differences between the two treatment groups in the distribution of time across pens, and these shifts were exactly opposite to those found for males. Experimental females spent less time in the female's home area and more time in both areas inhabited by males than did

Table 10. Mean Time Spent and Mean Tongue Extrusions Performed in Each of the Four Pens. Females, Experiment 1.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TIME (MIN)				
Control (n=15)	8.8 ± 13.4	6.7 ± 10.8	7.8 ± 9.8	6.7 ± 11.5
Experimental (n=15)	5.6 ± 9.9	10.0 ± 12.5	11.9 ± 12.9	2.5 ± 6.9
TONGUE EXTRUSIONS				
Control (n=15)	1.3 ± 2.3	0.5 ± 1.1	1.7 ± 3.1	0.7 ± 1.4
Experimental (n=15)	0.7 ± 1.6	1.1 ± 1.8	2.5 ± 4.9	0.4 ± 0.8

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

controls. Experimental females also spent less time in the empty pen than did control females.

Number of tongue extrusions. Tongue extrusions performed by control and experimental females did not differ as markedly as was the case for males. The number of extrusions made by experimental females was only slightly higher than that demonstrated by controls and neither the main effects (Pen: $F(3,112)=2.25$, ns; Condition: $F(1,112)=0.09$, ns) nor the interaction between pen and condition ($F(3,112)=0.55$, ns) were significant. Nevertheless, control and experimental distributions of tongue extrusions among the four pens differed and this difference (with the exception of the juvenile male's pen) moved in the opposite direction of that found for male distributions. Compared to controls, the number of extrusions performed by experimental females dropped in the adult female's pen, increased in the adult male's pen and in the juvenile male's pen, and decreased in the empty pen (see Table 10).

Rate of extruding. Compared to controls, the rate at which experimental females extruded the tongue rose in the adult male's pen and in the empty pen, while remaining virtually unchanged in the adult female's area and in the pen inhabited by the juvenile male (see Table 11). Neither the main effects (Pen: $F(3,112)=0.05$, ns; Condition: $F(1,112)=1.42$, ns) nor the interaction between pen and condition ($F(3,112)=0.76$, ns) were significant, however.

Table 11. Mean Number of Tongue Extrusions Performed Per Minute in Each of the Four Pens. Females, Experiment 1.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
Control (n=15)	.19 ± .23	.12 ± .07	.21 ± .23	.14 ± .04
Experimental (n=15)	.17 ± .15	.25 ± .51	.20 ± .16	.26 ± .36

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Marking. While control and experimental males showed distinct differences in marking behaviors, no such differences were found for female subjects. Moreover, the slight differences that did occur between female treatment groups were evenly distributed among the four pens (see Table 12).

Neither the difference in numbers of combined marking behaviors made by control and experimental females nor the interaction between pen and condition was significant (Pen: $F(3,112)=0.27$, ns; Condition: $F(1,112)=1.62$, ns; Interaction: $F(3,112)=0.27$, ns). The number of individuals performing marking attempts was similar in the two groups (two control and three experimental subjects, $P>0.10$, Fisher Exact Probability Test). When the three marking categories are examined separately, there are again no differences between control and experimental results either in terms of the number of behaviors demonstrated or in the number of individuals performing them.

Seconds spent bobbing. While experimental females spent somewhat more time bobbing than did controls, there were no significant differences between the two groups (Pen: $F(3,112)=0.36$, ns; Condition: $F(1,112)=0.16$, ns; Interaction: $F(3,112)=1.05$, ns).

The number of seconds spent bobbing while extruding the tongue were virtually the same for control and experimental females. There were no significant main effects

Table 12. Total Marking Behaviors Performed in Each of the Four Pens: Defecations (DEF), Pelvic Rubs (PR), and Chin Wipes (CW). Females, Experiment 1.

	Pen 1 (Adult Female Pen)			Pen 2 (Adult Male Pen)			Pen 3 (Juvenile Male Pen)			Pen 4 (Empty Pen)		
	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW
Control (n=15)	0	0	0	0	0	1	0	0	0	0	0	1
Experimental (n=15)	0	0	2	1	0	0	1	0	0	1	1	0

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

(Pen: $F(3,112)=0.35$, ns: Condition: $F(1,112)=0.12$, ns) and no significant interaction ($F(3,112)=0.57$, ns) (see Tables 13 and 14).

Number of pens entered. Control females entered a mean number of 1.6 pens while experimental females entered a mean of 2.1 pens ($t(28)=1.49$, ns). One control and one experimental female sampled all four pens.

Pen entered first. Compared to controls, experimental females were much more likely to enter Pen 2 first (the adult male's area) and much less likely to enter Pen 1 first (the adult female's area). The initial responses of control and experimental females to Pen 3 (the juvenile male's pen) and to Pen 4 (the empty pen) were almost identical (see Table 15).

Male/Female Comparisons

Males and females differed distinctly in several respects. Males extruded the tongue significantly more often than did females in both the control condition ($t(28)=2.51$, $P<0.05$) and in the experimental condition ($t(28)=3.09$, $P<0.01$) (see Table 16). Although control males and females were remarkably similar in marking behavior (a total of one chin wipe and two chin wipes, respectively), experimental males made more total marking attempts ($t(28)=1.70$, $P<0.10$) and more pelvic rubs ($t(28)=1.79$, $P<0.10$) than did experimental females.

In contrast, there were no significant differences in the time males and females spent performing bobbing

Table 13. Mean Total Seconds Spent Bobbing and Mean Seconds Bobbing in Association with Tongue Extrusions in Each of the Four Pens.
Females, Experiment 1.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TOTAL BOBBING				
Control (n=15)	3.3 ± 6.0	1.7 ± 4.1	2.1 ± 3.7	4.9 ± 11.8
Experimental (n=15)	3.3 ± 7.0	2.7 ± 5.8	5.7 ± 8.0	2.3 ± 5.7
BOBBING WITH TONGUE EXTRUSIONS				
Control (n=15)	0.7 ± 1.4	0.2 ± 0.8	0.9 ± 1.9	0.7 ± 2.1
Experimental (n=15)	0.3 ± 0.7	0.7 ± 2.3	0.7 ± 1.2	0.3 ± 1.3

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Table 14. Mean Seconds Spent Bobbing and Mean Seconds Bobbing In Association With Tongue Extrusions. Females, Experiment 1.

	Seconds Spent Bobbing	Seconds Bobbing In Association With Tongue Extrusions
Control (n=15)	12.0 ± 15.3	2.5 ± 3.8
Experimental (n=15)	14.0 ± 10.3	2.1 ± 2.6

Table 15. Release Procedure and Initial Pen Preference. Females, Experiment 1.

	Release Procedure		First Pen Entered
	Observer Exited	Subject Facing	Number of Subjects Entering Pen First
Control			
Pen 1	5	5	5
Pen 2	3	4	4
Pen 3	5	2	4
Pen 4	2	4	2
Experimental			
Pen 1	4	3	1
Pen 2	4	4	9
Pen 3	3	4	4
Pen 4	4	4	1

Table 16. Comparison of Tongue Extrusions, Marking, and Time Spent Bobbing by Male and Female Subjects (Mean±SD). Experiment 1.

	MALES	FEMALES	
Tongue Extrusions			
Control (n=15)	10.5 ± 8.6	4.2 ± 4.4	P<0.05
Experimental (n=15)	16.7 ± 14.2	4.7 ± 4.9	P<0.01
Seconds Spent Bobbing			
Control (n=15)	12.7 ± 15.4	12.0 ± 15.3	
Experimental (n=15)	12.1 ± 10.3	14.0 ± 10.3	
Seconds Bobbing In Association With Tongue Extrusions			
Control (n=15)	3.2 ± 4.4	2.5 ± 3.8	
Experimental (n=15)	3.1 ± 3.7	2.1 ± 2.6	
Marking (All Categories)			
Control (n=15)	0.1 ± 0.3	0.1 ± 0.4	
Experimental (n=15)	1.3 ± 1.9	0.4 ± 0.9	P<0.10
Pelvic Rubs			
Control (n=15)	0.0 ± 0.0	0.0 ± 0.0	
Experimental (n=15)	0.8 ± 1.6	0.1 ± 0.3	P<0.10

displays in either the control or experimental condition (Two-way ANOVA. Sex: $F(1,56)=0.03$, ns; Condition: $F(1,56)=0.04$, ns; Interaction: $F(1,56)=0.15$, ns) nor did males and females differ significantly in terms of bobbing performed in conjunction with tongue extrusions in either treatment condition (Sex: $F(1,56)=0.76$, ns; Condition: $F(1,56)=0.06$, ns; Interaction: $F(1,56)=0.03$, ns) (see Table 16).

Discussion

If chemicals from conspecifics influence the social behavior of *S. jarrovi*, we might expect breeding males traveling outside their own territories to be attracted to an area containing chemicals left by an adult female and, particularly in the case of this highly territorial species, to avoid an area containing chemicals deposited by another adult male.

The significant differences in the distributions of tongue extrusions made by control and experimental subjects indicate that males can detect the chemicals deposited by conspecifics and can determine the sex of the depositor. Increases in the tongue extrusions and marking behaviors performed in the adult female's pen suggest that males are, in fact, attracted to areas containing female deposits, while a decrease in the tongue extrusions performed in the adult male's pen may indicate that males avoid areas containing the deposits of another male. [1]

The data in terms of the time spent in the four pens by control and experimental males show trends which support these hypotheses. Had observation periods permitted the animals sufficient time to sample all four areas, preferences in terms of time might have been clearer.

As male S. jarrovi are the more aggressive sex in mating (both in adjusting the location of their territories to encompass females and in initiating courtship), females were not expected to show as strong an attraction as males to an area containing the chemicals deposited by an adult of the opposite sex. If chemicals from conspecifics influence the social behavior of females, however, they, like males, should avoid an area containing chemicals deposited by an adult of the same sex. Although support for this hypothesis is weak, the fact that females distributed time and tongue extrusions among the four pens in a manner which was exactly opposite that demonstrated by male subjects suggests that females may also respond

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[1] Due to problems in the release procedure, there was some concern that the baseline data for control males might have been confounded. Careful analysis of the data, however, indicates that this was not the case. Comparisons of the first and second halves of each condition showed no significant intra-group differences in either the number of tongue extrusions performed or the time spent in each pen. Control and experimental males in both Experiments 1 and 3 indicated an initial preference for Pen 2 regardless of the direction in which the subject faced when released or the direction from which the observer exited. The subsequent responses to the four pens discussed above, however, differed as a function of treatment condition, indicating that the behavior of experimental males was influenced by the different chemicals deposited in the four areas.

to conspecific chemical signals.

The depositing of male chemicals appears to involve both pelvic rubbing and defecations. As pelvic rubbing includes contact of the inside of the leg and the entire pelvic area with the substrate, both the cloaca and the femoral pores could be sources of the chemicals deposited by males. While it is possible that the chemicals involved all originate in the cloacal area, the significant increase in pelvic rubbing by males (whose femoral pores increase in size and secrete during the breeding season) and the virtual absence of pelvic rubbing by females (whose femoral pores are smaller than those of males and do not show seasonal changes) indicate that at least some of the chemicals deposited by males were probably provided by these pores. Female subjects showed no specific behaviors which could be connected with the depositing of chemicals.

The chemical cues used by S. jarrovi seem to be perceptible only at a short distance. While increased tongue extruding and marking in the adult female's pen indicate that males were quite attracted to her area, only one experimental male entered this pen first, thus implying that males were unable to detect female chemical deposits from a distance of only a few feet. This inference is consistent with recent suggestions that the vomeronasal system is used primarily for the detection of non-volatile compounds (Burghardt, 1980).

Finally, there is no evidence that conspecific chemicals function to release visual displays in S. jarrovi. Since Duvall's work with S. occidentalis indicated a close connection between detection of chemicals deposited by conspecifics and subsequent performance of bobbing displays, it may be that closely related sceloporine species are very different in this regard.

CHAPTER IV

EXPERIMENT 2

As Sceloporus jarrovi are generally territorial throughout the active period of May-October, adult males traveling outside their own territories might be expected to avoid an area containing the chemical deposits of another adult male in the spring months as well as in the fall. In contrast to their behavior during breeding months, however, males would not be expected to be particularly attracted to an area containing female deposits in the spring.

Although the data obtained in Experiment 1 provided little evidence that adult females respond to chemicals left by conspecifics of either sex, this may have been due to seasonal differences in the territorial behavior of males and females rather than an indication that females do not utilize conspecific chemical information. While male territorial behavior increases in the fall, females establish permanent territories in May and female aggression drops in the fall. Thus, if female S. jarrovi do avoid an area containing chemicals left by another adult female, this behavior is likely to be more pronounced in the spring months than in the fall.

The following experiment was designed to investigate the response of S. jarrovi to chemicals deposited by conspecifics during the spring months.

Methods

Subjects

Fifteen male and 15 female adult S. jarrovi served as control subjects. All but two of the control females were visibly gravid. Fifteen adult males and 15 adult females also comprised the experimental group. As births in the study area occurred from late May through June, some of the female experimental subjects were still gravid at the time of testing while others had already given birth. Five males and eight females served in both control and experimental conditions, but no subject was tested more than once in each condition.

Procedure

Control. Prior to the introduction of the resident animals, the 30 control subjects were tested to establish baseline data for the four pens. The control procedure was identical to that described in Experiment 1 with one exception - the release patterns for male and female subjects were the same, with the direction in which the subject faced and the direction from which the observer exited balanced evenly among the four pens. Subjects were tested from May 5 - May 22, 1979.

Experimental. Following completion of the control condition, the board dividers were placed in the enclosure, separating the area into four pens. The pens used to house animals in Experiment 1 were each chosen to house

a similar animal in this experiment, with an adult female (s-v length 8.0 cm) in Pen 1, an adult male (s-v length 7.2 cm) in Pen 2, and a juvenile male (s-v length 4.8 cm) in Pen 3. Pen 4 was again left empty. (See Figure 1.)

The adult female resident was gravid when first placed in the enclosure and remained so throughout the experimental condition. As the resident animals were first placed in the enclosure in late May before females had begun giving birth, there was not yet a current juvenile population from which to pick a resident juvenile animal. The resident juvenile male was therefore taken from Rustler Park, a nearby area in the Chiricahua Mountains, where he had been born the previous summer. At this altitude (2,560 meters), S. jarrovi are born in July, a month later than in the study area, and thus do not reach maturity by their first fall breeding season. On this basis, and on the basis of his s-v length of 4.8 cm, the Rustler Park male resident was considered a juvenile. By the end of the experimental condition, he had grown to only 5.2 cm, still below the minimum length of 5.5 cm at which Goldberg (1971) found sexually mature males.

Resident lizards were allowed to inhabit their pens for 6 days before any testing of experimental subjects was undertaken.

Experimental animals were tested from May 30 -

June 27, 1979. The testing procedure and data collection were identical to that described for the experimental condition of Experiment 1. The release patterns for males and females duplicated those used in the control condition.

Results

Possible Effects of Subject Chemical Deposits

For both experimental males and experimental females, there were no significant differences between Long Delay and Short Delay Groups in terms of either mean number of tongue extrusions (Males: $t(12)=1.75$, ns; Females: $t(13)=0.40$, ns) or mean overlap time (Males: $t(12)=0.17$, ns; Females: $t(13)=0.94$, ns). When the two subjects (one male and one female) which followed a subject of the same sex were excluded from analysis, the difference between the Long Delay and Short Delay Groups remained insignificant.

Control subjects were not analyzed in terms of possible response to the preceeding subject because of a problem in the control procedure. When testing of the control animals began, births had not yet occurred during the current year so any animals present were a year old and thus considered to be adult. After the decision to use the Rustler Park male born the previous year as the juvenile male resident, those control subjects with a s-v length of less than 6.0 cm (four males and three females) were eliminated and seven new control subjects

were tested prior to placing the resident animals in their pens. As a result, several of the control subjects were preceeded by animals later defined as juveniles and, therefore, any analysis of the response of subjects to the chemicals of previous subjects might be clouded by differences in the sexual maturity of those previous subjects.

Nevertheless, the experimental data indicate that in the spring as during the preceeding fall, neither the number of tongue extrusions a subject performed in a pen nor the time it spent in an area was significantly influenced by any chemicals which might have been left by the immediately preceeding subject.

Responses to Resident Chemical Deposits

Comparison of Control vs. Experimental Conditions

Males.

Time spent in each pen. If S. jarrovi respond to the chemicals deposited by conspecifics, we would expect experimental males to spend less time than controls in the adult male's pen. In contrast to breeding males, however, experimental males tested in the spring would not be expected to show an increase in the time spent in the female's area.

A two-way ANOVA of the time spent in each pen showed no significant main effects (Pen: $F(3,112)=1.58$, ns; Condition: $F(1,112)=0.00$, ns) and no significant interaction between pen and condition ($F(3,112)=1.95$, ns). As Table 17 illustrates, the data do not even suggest a trend in the

Table 17. Mean Time Spent and Mean Tongue Extrusions Performed in Each of the Four Pens. Males, Experiment 2.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TIME (MIN)				
Control (n=15)	13.3 ± 13.5	8.5 ± 11.2	4.0 ± 9.2	4.1 ± 9.4
Experimental (n=15)	7.2 ± 12.7	7.1 ± 9.9	11.4 ± 12.0	4.2 ± 8.7
TONGUE EXTRUSIONS				
Control (n=15)	2.1 ± 3.0	1.0 ± 1.4	0.5 ± 1.2	1.1 ± 2.5
Experimental (n=15)	0.9 ± 2.6	1.0 ± 1.8	1.8 ± 2.9	0.3 ± 0.7

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

direction predicted. While experimental males spent less time than controls in both the adult male's home area and in the pen inhabited by the adult female, the decrease was considerably greater in the female's pen than in the adult male's area. The largest difference in the times experimental and control males spent in a particular pen occurred in the area inhabited by the juvenile male. Experimental males spent virtually the same amount of time in the empty pen as did controls.

Number of tongue extrusions. A two-way ANOVA showed no significant main effects (Pen: $F(3,112)=0.65$, ns; Condition: $F(1,112)=0.21$, ns) and no significant interaction between pen and condition ($F(3,112)=2.06$, ns). As seen in Table 17, the number of extrusions dropped in the female's home area and in the empty pen and increased in the pen occupied by the juvenile male. The number of tongue extrusions made by experimental males in the adult male's pen was identical to the number demonstrated by control males.

Rate of extruding. When male tongue extrusions are examined in terms of rate of occurrence, we again find no significant differences between control and experimental performances (Pen: $F(3,112)=0.40$, ns; Condition: $F(1,112)=2.61$, ns; Interaction: $F(3,112)=1.10$, ns). As seen in Table 18, the rates of extruding by control and experimental animals were virtually the same in both the adult

Table 18. Mean Number of Tongue Extrusions Performed Per Minute in Each of the Four Pens. Males, Experiment 2.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
Control (n=15)	.29 ± .50	.15 ± .12	.17 ± .17	.23 ± .22
Experimental (n=15)	.13 ± .07	.14 ± .11	.18 ± .21	.11 ± .10

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

male's pen and in the juvenile male's pen. Experimental males extruded the tongue at a lower rate than controls in the female's area and in the empty pen.

Marking. Unlike the previous fall, males performed few possible marking attempts of any kind in the spring (see Table 19). Control males demonstrated only one defecation and one chin wipe and experimental males only two defecations and two chin wipes. Neither group performed pelvic rubs. The number of individuals that marked was correspondingly low (two control males and three experimental males).

Seconds spent bobbing. Experimental males showed a significant decrease in total bobbing when compared to controls ($F(1,112)=4.63$, $P<0.05$). However, neither the pen effect ($F(3,112)=0.78$, ns) nor the interaction between pen and condition ($F(3,112)=1.20$, ns) was significant (see Tables 20 and 21).

There were no significant differences between control and experimental males in terms of bobbing performed in conjunction with tongue extrusions (Pen: $F(3,112)=0.27$, ns; Condition: $F(1,112)=0.39$, ns; Interaction: $F(3,112)=1.74$, ns).

Number of pens entered. Control males entered a mean number of 2.1 pens, while experimental males entered a mean of 1.8 pens ($t(28)=0.93$, ns). No animal in either group entered all four pens.

Table 19. Total Marking Behaviors Performed in Each of the Four Pens: Defecations (DEF), Pelvic Rubs (PR), and Chin Wipes (CW). Males, Experiment 2.

	Pen 1 (Adult Female Pen)			Pen 2 (Adult Male Pen)			Pen 3 (Juvenile Male Pen)			Pen 4 (Empty Pen)		
	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW
Control (n=15)	1	0	0	0	0	1	0	0	0	0	0	0
Experimental (n=15)	0	0	1	1	0	1	0	0	0	1	0	0

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Table 20. Mean Total Seconds Spent Bobbing and Mean Seconds Bobbing in Association with Tongue Extrusions in Each of the Four Pens.
Males, Experiment 2.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TOTAL BOBBING				
Control (n=15)	2.0 ± 2.8	2.0 ± 4.4	1.1 ± 2.5	0.5 ± 1.2
Experimental (n=15)	0.4 ± 1.3	0.1 ± 0.3	1.2 ± 3.2	0.2 ± 0.6
BOBBING WITH TONGUE EXTRUSIONS				
Control (n=15)	0.4 ± 1.1	0.3 ± 0.8	0.1 ± 0.3	0.1 ± 0.5
Experimental (n=15)	0.0 ± 0.0	0.1 ± 0.3	0.5 ± 1.4	0.1 ± 0.3

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Table 21. Mean Seconds Spent Bobbing and Mean Seconds Bobbing In Association With Tongue Extrusions. Males, Experiment 2.

	Seconds Spent Bobbing	Seconds Bobbing In Association With Tongue Extrusions
Control (n=15)	5.7 ± 5.9	0.9 ± 1.3
Experimental (n=15)	1.9 ± 3.5	0.6 ± 1.5

Pen entered first. In Experiment 2, the number of times subjects were released facing each pen and the number of times the observer exited from each pen were the same for both control and experimental animals. Therefore, the data were not analyzed to the degree necessary in Experiment 1. Control and experimental males did not show any noticeable differences in which pens they entered first (see Table 22).

Females

Time spent in each pen. If S. jarrovi respond to the chemical deposits of conspecifics, we would expect experimental females to spend less time than controls in the pen inhabited by the adult female. However, a two-way ANOVA of the time spent in each pen showed no significant differences between control and experimental groups (Pen: $F(3,112)=0.60$, ns; Condition: $F(1,112)=0.00$, ns; Interaction: $F(3,112)=0.35$, ns).

The data not only failed to support this hypothesis but in addition showed a trend in the opposite direction. The time experimental females spent relative to controls actually increased in the adult female's home area and decreased in the adult male's pen. Differences between the times control and experimental females spent in the juvenile male's pen and in the empty pen were slight (see Table 23).

Number of tongue extrusions. As shown in Table 23,

Table 22. Release Procedure and Initial Pen Preference. Males, Experiment 2.

	Release Procedure*		First Pen Entered	
	Observer Exited	Subject Facing	Number of Control Subjects Entering Pen First	Number of Experimental Subjects Entering Pen First
Pen 1	4	4	3	3
Pen 2	4	3	5	3
Pen 3	4	4	4	4
Pen 4	3	4	3	5

*Control and Experimental Conditions Were Identical.

Table 23. Mean Time Spent and Mean Tongue Extrusions Performed in Each of the Four Pens. Females, Experiment 2.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TIME (MIN)				
Control (n=15)	6.5 ± 10.9	9.0 ± 12.1	5.3 ± 8.4	9.2 ± 12.1
Experimental (n=15)	9.1 ± 13.4	5.8 ± 11.1	5.6 ± 9.0	9.5 ± 11.4
TONGUE EXTRUSIONS				
Control (n=15)	0.9 ± 1.5	1.4 ± 2.2	0.8 ± 1.3	1.3 ± 2.7
Experimental (n=15)	0.5 ± 1.3	0.1 ± 0.4	0.5 ± 1.1	0.6 ± 1.6

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

experimental females made significantly fewer tongue extrusions than did control females ($F(1,112)=4.89$, $P<0.05$) but the decrease was spread relatively evenly across pens with no pen receiving an increase in extrusions (Pen: $F(3,112)=0.20$, ns; Interaction: $F(3,112)=0.50$ ns).

Rate of extruding. As the time per observation period was held constant, a decrease in the number of tongue extrusions performed by experimental females as compared to controls would necessarily result in a comparable drop in the rate of extruding ($F(1,112)=14.46$, $P<0.01$). Again, however, there was no significant pen effect and no significant interaction between pen and condition (Pen: $F(3,112)=0.69$, ns; Interaction: $F(3,112)=0.33$, ns). (See Table 24).

Marking. Female subjects demonstrated the same low rate of marking as did males (see Table 25). Control females made two defecations and one pelvic rub, while experimental females performed only one pelvic rub. Neither group made any chin wipes. The number of individuals performing these behaviors was correspondingly low (two control females and one experimental female).

Seconds spent bobbing. Like males, experimental females also showed a significant decrease in total bobbing when compared to controls ($F(1,112)=5.47$, $P<0.05$) but neither the pen effect ($F(3,112)=0.37$, ns) nor the interaction between pen and condition ($F(3,112)=0.24$, ns) was significant (see Tables 26 and 27).

Table 24. Mean Number of Tongue Extrusions Performed Per Minute in Each of the Four Pens. Females, Experiment 2.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
Control (n=15)	.19 ± .16	.13 ± .09	.16 ± .13	.20 ± .28
Experimental (n=15)	.08 ± .13	.05 ± .02	.08 ± .14	.06 ± .07

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Table 25. Total Marking Behaviors Performed in Each of the Four Pens: Defecations (DEF), Pelvic Rubs (PR), and Chin Wipes (CW). Females, Experiment 2.

	Pen 1 (Adult Female Pen)			Pen 2 (Adult Male Pen)			Pen 3 (Juvenile Male Pen)			Pen 4 (Empty Pen)		
	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW
Control (n=15)	1	1	0	0	0	0	0	0	0	1	0	0
Experimental (n=15)	0	0	0	0	0	0	0	1	0	0	0	0

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Table 26. Mean Total Seconds Spent Bobbing and Mean Seconds Bobbing in Association with Tongue Extrusions in Each of the Four Pens.
Females, Experiment 2.

	Pen 1 (Adult Female Pen)	Pen 2 (Adult Male Pen)	Pen 3 (Juvenile Male Pen)	Pen 4 (Empty Pen)
TOTAL BOBBING				
Control (n=15)	1.5 ± 3.1	1.6 ± 3.2	2.2 ± 4.6	2.9 ± 5.9
Experimental (n=15)	0.6 ± 1.1	0.7 ± 1.2	0.6 ± 1.4	0.8 ± 2.4
BOBBING WITH TONGUE EXTRUSIONS				
Control (n=15)	0.2 ± 0.4	0.3 ± 0.7	0.6 ± 1.3	0.1 ± 0.5
Experimental (n=15)	0.3 ± 0.8	0.0 ± 0.0	0.1 ± 0.3	0.1 ± 0.5

Note: Pens are designated by experimental resident animal for the sake of clarity. All pens were empty in the control condition.

Table 27. Mean Seconds Spent Bobbing and Mean Seconds Bobbing In Association With Tongue Extrusions. Females, Experiment 2.

	Seconds Spent Bobbing	Seconds Bobbing In Association With Tongue Extrusions
Control (n=15)	8.3 ± 7.8	1.2 ± 1.7
Experimental (n=15)	2.7 ± 4.2	0.5 ± 1.2

There were no significant differences between control and experimental females in terms of bobbing performed in conjunction with tongue extrusions (Pen: $F(3,112)=0.66$, ns; Condition: $F(1,112)=1.84$, ns; Interaction: $F(3,112)=1.45$, ns).

Number of pens entered. Control females entered a mean number of 2.1 pens, with one female entering all four pens. Experimental females entered a mean of 1.8 pens, again with one female sampling all four pens ($t(28)=0.80$, ns).

Pen entered first. The release procedure used for males was duplicated for females. Control and experimental females did not show any noticeable differences in which pen they entered first (see Table 28).

Male/Female Comparisons

The differences between males and females in tongue extruding and marking behaviors noted during the breeding season were not present in the spring. There were no significant differences in the number of tongue extrusions performed by males and females in either the control condition ($t(28)=0.27$, ns) or the experimental condition ($t(28)=1.80$, ns) (see Table 29). Marking by both males and females was minimal in each of the two treatment conditions.

Similar to the previous fall, there were no differences in the number of seconds spent bobbing as a function

Table 28. Release Procedure and Initial Pen Preference. Females, Experiment 2.

	Release Procedure*		First Pen Entered	
	Observer Exited	Subject Facing	Number of Control Subjects Entering Pen First	Number of Experimental Subjects Entering Pen First
Pen 1	4	4	4	5
Pen 2	4	3	5	4
Pen 3	4	4	3	2
Pen 4	3	4	3	4

*Control and Experimental Conditions Were Identical.

Table 29. Comparison of Tongue Extrusions, Marking, and Time Spent Bobbing by Male and Female Subjects (Mean±SD). Experiment 2.

	MALES	FEMALES
Tongue Extrusions		
Control (n=15)	4.7 ± 3.9	4.3 ± 4.3
Experimental (n=15)	4.0 ± 4.2	1.7 ± 2.8
Seconds Spent Bobbing		
Control (n=15)	5.7 ± 5.9	8.3 ± 7.8
Experimental (n=15)	1.9 ± 3.5	2.7 ± 4.2
Seconds Bobbing In Association With Tongue Extrusions		
Control (n=15)	0.9 ± 1.3	1.2 ± 1.7
Experimental (n=15)	0.6 ± 1.5	0.5 ± 1.2
Marking (All Categories)		
Control (n=15)	0.1 ± 0.4	0.2 ± 0.6
Experimental (n=15)	0.3 ± 0.6	0.1 ± 0.3
Pelvic Rubs		
Control (n=15)	0.0 ± 0.0	0.1 ± 0.3
Experimental (n=15)	0.0 ± 0.0	0.1 ± 0.3

of sex, although experimental subjects of both sexes spent significantly less time bobbing than did controls (Sex: $F(1,56)=1.38$, ns; Condition: $F(1,56)=10.56$, $P<0.01$; Interaction: $F(1,56)=0.39$, ns). Compared to controls, experimental subjects also bobbed less in conjunction with tongue extrusions. Again, however, there were no significant differences between male and female subjects (Sex: $F(1,56)=0.07$, ns; Condition: $F(1,56)=1.86$, ns; Interaction: $F(1,56)=0.21$, ns) (see Table 29).

Discussion

It was suggested that, in the spring as well as the fall, both male and female adults might avoid areas outside their own territories which contained chemicals deposited by another adult of the same sex. In fact, it was suspected that females would be more likely to demonstrate this response in the spring, when they establish permanent territories, than in the fall, when female-female aggression drops. On the other hand, the attraction demonstrated by males in the fall to an area containing female deposits was not expected in the spring.

Contrary to my hypothesis, the results for both males and females provide no evidence that *S. jarrovi* avoid areas containing the chemical deposits of other same-sex adults in the spring months. In fact, if the data suggest anything at all, it is possibly an indifference to the area occupied by a same-sex adult and a slight avoidance of an

area in which an opposite-sex adult resides.

The only statistically significant results obtained concern the decrease in time spent bobbing demonstrated by experimental males and experimental females and the decrease in number of total tongue extrusions and overall rate of extruding demonstrated by experimental females. Since analyses of these data showed no significant interactions between pen and condition, it appears that the decreases noted in these behaviors were not a function of the chemicals deposited by residents in the four areas.

The decrease in behaviors performed by females may have been part of a general decline in their activity from higher levels at the beginning of the season to lower levels in the fall. However, other data conflict with this interpretation. First, the number of tongue extrusions, the seconds spent bobbing, and the bobbing seconds associated with tongue extruding performed by control and experimental females the previous fall were each higher than the numbers demonstrated by either control or experimental females in the spring. Thus, a simple linear decline in female activity is not a sufficient explanation for the control and experimental differences in female tongue extruding and bobbing found in this experiment. Secondly, while all female activities measured showed some reduction when experimental and control results were compared, the same was true for the behaviors demonstrated

by males. Since presumably male activity increases as the season progresses, it appears that the animals in this experiment were responding to something other than seasonal patterns of behavior.

An alternative explanation may lie in the increase in temperature which occurred between control and experimental testing. The maximum temperatures on control test days ranged from 69°-84°, with an average of 79°, while the maximum temperatures on experimental test days ranged from 74°-95°, with an average of 84°. Moreover, due to seasonal shifts in the position of the sun, experimental animals had to be tested around mid-day when the sun/shade mosaic was evenly distributed among the four pens. A greater leeway was possible in the hours in which control subjects could be tested. These increased temperatures may have forced experimental subjects to seek shelter more often than controls. If this were the case, exploratory activity would necessarily have been reduced for both sexes. As females were either still gravid or had recently given birth, perhaps they were more vulnerable to extreme temperatures than were males.

The results of Experiment 2 clearly indicate that during the spring and early summer, active marking by both males and females is minimal. Of particular interest is the total lack of male pelvic rubbing in contrast to the high rate of rubbing demonstrated during the breeding sea-

son. This further supports the premise that the sexually dimorphic femoral pores function in the mating behavior of males.

There is no evidence that chemicals deposited by conspecifics served to release visual displays performed in the spring.

CHAPTER V

EXPERIMENT 3

The results obtained in Experiment 1 indicate that breeding males can detect chemicals deposited by female conspecifics and are attracted to an area containing these deposits. Clearly, it is advantageous for breeding males to be able to locate female conspecifics by chemical as well as visual means. If males could, in addition, distinguish the deposits left by sexually mature females from those left by juvenile females, this ability would aid them not only in locating potential mates but in focusing courtship on those females most likely to be reproductive. Chemical information of this sort would be especially important in cases where visual information is insufficient.

The reproductive status of those females who have just reached maturity may be difficult to determine by visual cues alone. Of the females born in the spring at low altitudes, 60% of the survivors will reach maturity by the following fall breeding season. As there is no significant difference between the sizes of mature yearling females and immature yearling females (Ballinger, 1973), male animals may not be able to differentiate between small adult and large juvenile females on the basis of size alone. Behavioral information may also be incomplete. Juvenile females respond to male displays by run-

ning away. However, except for the brief period in which they are sexually receptive, adult females respond to courting males in a similar manner. Males are therefore faced with the problem of having to invest considerable time courting a female before she actually becomes receptive, while her behavior provides no reliable gauge for determining whether she is even potentially reproductive. Chemical cues could provide the extra information necessary for males to make this discrimination, particularly in the case of small females.

Experiment 3 was designed to determine whether adult males could distinguish between the chemicals deposited during the breeding season by adult females and those deposited by sexually immature/juvenile females.

Methods

Subjects

Thirty adult male S. jarrovi comprised the control group. As in Experiment 1, the control subjects were tested in late August, so presumably they had not mated since the previous fall. The 30 adult males comprising the experimental group were tested during the breeding months of September and October and may or may not have mated at the time of testing. Ten individuals served in both conditions, but none was tested more than once per condition.

Procedure

Control. Prior to the introduction of resident animals, the 30 control subjects were tested to establish baseline data for the four pens. The procedure followed was identical to the control procedure described earlier, with the direction the subject faced and the direction from which the observer exited evenly balanced across pens. Care was taken to test the Fall 1979 control subjects during the same calandar period (8/19-8/31) as control subjects for the 1978 breeding season had been tested, in the hope that later comparisons of the results of Experiments 1 and 3 would not be confounded by slight seasonal variations.

Experimental. Following completion of the control condition, the board dividers were placed in the enclosure, forming four separate pens. Three of these pens were established as home areas for resident S. jarrovi. Pen 4 was inhabited by an adult female, Pen 3 by a single juvenile female, and Pen 2 by two juvenile females.[1] Pen 1

[1] If males can distinguish between the deposits of adult and juvenile females, this discrimination could be based on qualitative differences in the substances, quantitative differences in amounts deposited, or some combination of qualitative and quantitative differences. If qualitative differences are involved, responses made to Pen 4 (adult female) should be greater than to other pens. If quantitative differences are involved, responses to Pen 2 (two juvenile females) should be greater than to Pen 3 (one juvenile female). If discriminations involve both qualitative and quantitative differences, we might expect response levels to diminish from Pen 4 (adult female) to Pen 2 (two juvenile females) to Pen 3 (one juvenile female).

was left empty. (See Figure 2.)

An examination of the male control results for the fall of both 1978 and 1979 indicated that Pen 4 might be a less attractive site than the others, at least during the fall months. Although the differences between this pen and the other three were not statistically significant, in both years the lowest percentages of total male control tongue extrusions were performed there (1978: 8%; 1979: 9%) and the area was relatively unpopular in terms of the time control males spent there (1978: third in terms of time; 1979: fourth in terms of time).

While this was the pen left empty in the experimental conditions of Experiments 1 and 2, it was decided to place the adult female (presumably the most attractive resident) here in this experiment. The reasons for this change were two-fold. First, I wanted to see if the adult female's deposits would be attractive enough to overcome the pen's seeming unattractiveness. Secondly, a slight possibility existed that the increased interest displayed the previous fall by experimental males in the adult female's area had been influenced by seasonal changes beyond my control (such as a shift in the direction of sunlight as winter approached). Changing the adult female to another pen would serve as a control for this variable. For this reason also, the pen which had housed the adult female in Experiments 1 and 2 (Pen 1) was the pen left empty in this experiment.

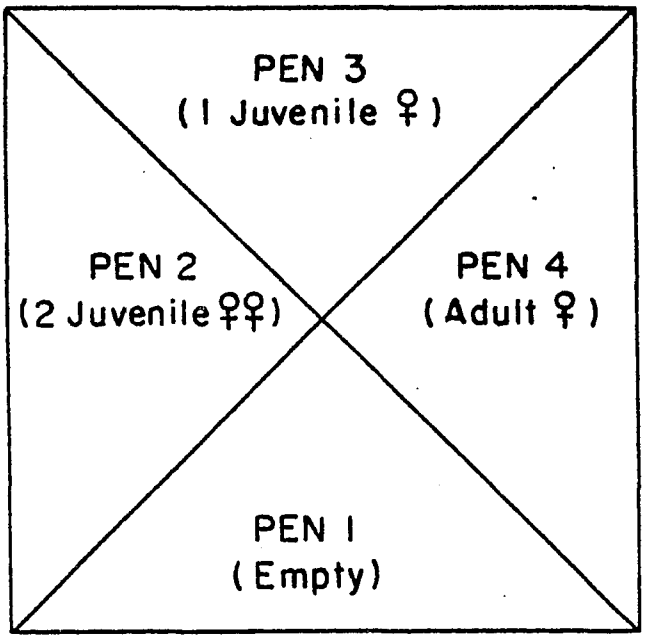

Figure 2. Experiment 3: Placement of the Resident Animals in the Four Pens.

Resident lizards were allowed to inhabit their pens for 5-6 days before any testing of experimental subjects was undertaken.

Experimental animals were tested during a five week period in the breeding months of September and October (9/9-10/12) 1979. Again, care was taken to test subjects during the same calendar period as the experimental subjects for the 1978 breeding season had been tested. The testing procedure was identical to that described for the experimental condition of Experiment 1. Control and experimental release patterns were identical, with the direction the subjects faced and the direction from which the observer exited evenly balanced across pens.

Unfortunately, during the course of the experiment, some of the resident animals had to be replaced. On the first test day, the single juvenile female (s-v length 4.5 cm) died and was replaced by another juvenile of the same length. I took this opportunity to also replace the adult female resident (s-v length 8.2 cm) with another animal (s-v length 7.6 cm). This was done because the original adult resident was extremely wary and rarely left the immediate area of a rock in the far corner of her pen. It was possible, therefore, that the major part of her pen would be unmarked. The new adult female resident, on the other hand, proved much more active, utilizing all of her home area. Testing was not resumed until the fifth day

following placement of the new animals in the enclosure to allow them sufficient time to adjust to their new surroundings. On the second test day, the new single juvenile was discovered missing from the enclosure and had to be replaced by a third single juvenile (s-v length 4.6 cm). The next test day was postponed until the seventh day following this replacement to assure that she would not escape or die in the pen. No further escapes or deaths occurred for the remainder of the experiment (8 test days). The two juveniles housed together (s-v lengths 4.8 cm and 5.0 cm) remained constant throughout the experiment.

To assure that the juvenile female residents had not grown to reproductive length during the course of the experiment, they were measured on the last test day. The s-v lengths of the three juveniles were 4.7 cm, 4.8 cm, and 5.2 cm. Thus none had reached 5.5 cm, the minimum length at which they could be considered adult (Goldberg, 1971).

Results

Possible Effects of Subject Chemical Deposits

Unlike the two previous experiments, the subjects in Experiment 3 were all males; therefore, data were not analyzed as to the sex of the preceeding subject.

There were no significant differences between experimental subjects in the Long Delay Group and Short Delay

Group in terms of mean tongue extrusions ($t(27)=1.81$, ns) or mean overlap time ($t(27)=0.32$, ns).

When control subjects in the Long Delay Group were compared with those in the Short Delay Group, there were again no significant differences in terms of mean tongue extrusions ($t(27)=1.21$, ns) or in mean overlap time ($t(27)=0.51$, ns).

Thus, in the case of both experimental and control animals, there was no evidence to indicate that subjects were influenced by the chemicals deposited by the immediately preceeding subject, either in terms of the number of tongue extrusions the animals performed in pens entered by the previous subject or in the time animals spent in pens the previous subject had frequented.

Responses to Resident Chemical Deposits

Comparison of Control vs. Experimental Conditions

Males.

Time spent in each pen. If breeding males can discriminate between the chemical deposits of adult females and those of sexually immature females, we would expect experimental males to spend significantly more time in the pen occupied by the adult female than controls and to show less of a difference from controls in the pens which housed juveniles. We would also expect them to spend less time in the empty pen than did controls. A two-way ANOVA

provided no support for these hypotheses (Pen: $F(3,232)=3.23$, $P<0.05$; Condition: $F(1,232)=0.00$, ns; Interaction: $F(3,232)=2.28$, ns).

The significant pen effect, however, complicates the data, suggesting that a particular pen (or pens) may be preferred regardless of whether or not the area is occupied by a resident animal. While a Student-Newman-Keuls test showed no one pen to be statistically different from the other three, an examination of the data (see Table 30) indicates that the area inhabited by the single juvenile (Pen 3) may have been intrinsically more attractive since both control and experimental subjects spent more time in this area than in any other pen.

Although there was no significant interaction between pen and condition, there were differences in the amount of time control and experimental males allotted to each of the four pens and these differences were generally compatible with the above hypotheses. Experimental males spent more time in the adult female's area than did controls and less time in the pen which remained empty. The two groups differed relatively little in the time spent in the pen housing the two juvenile females. Unexpectedly, however, experimental males showed a considerable increase compared to controls in the time spent in the single juvenile's home area. As this pen was the preferred area in terms of time spent in both control and experimental conditions, it

Table 30. Mean Time Spent and Mean Tongue Extrusions Performed in Each of the Four Pens. Males, Experiment 3.

	Pen 1 (Empty Pen)	Pen 2 (Two Juvenile Females)	Pen 3 (One Juvenile Female)	Pen 4 (Adult Female)
TIME (MIN)				
Control (n=30)	8.6 ± 12.7	8.3 ± 11.5	9.3 ± 11.6	3.8 ± 7.7
Experimental (n=30)	3.4 ± 7.0	7.2 ± 10.2	12.2 ± 11.2	7.1 ± 8.4
TONGUE EXTRUSIONS				
Control (n=30)	2.0 ± 3.6	1.6 ± 3.1	2.5 ± 5.2	0.6 ± 1.8
Experimental (n=30)	0.5 ± 1.0	2.2 ± 4.0	3.9 ± 3.8	4.0 ± 5.3

Note: Pens are designated by experimental resident animals for the sake of clarity. All pens were empty in the control condition.

is impossible to say whether this increase was in response to the chemicals deposited there or not.

Number of tongue extrusions. As can be seen from Table 30, experimental and control males responded very differently to the four pens in terms of the number of tongue extrusions demonstrated. Experimental males made a greater total number of extrusions (319) than did controls (200) and they distributed these extrusions among the four pens differently than did controls. A two-way ANOVA showed that both of the main effects (Pen: $F(3,232)=2.96$, $P<0.05$; Condition: $F(1,232)=4.24$, $P<0.05$) and the interaction between pen and condition ($F(3,232)=4.48$, $P<0.01$) were significant. An analysis of the simple main effects showed that this significant interaction was due to a significant increase in the number of extrusions performed in the pen housing the adult female ($F(1,58)=10.96$, $P<0.01$) and a significant decrease in the empty pen ($F(1,58)=5.20$, $P<0.05$). The interaction between pen and condition was not significant in either the pen housing the single juvenile female ($F(1,58)=1.51$, ns) or in the pen in which the two juvenile females resided ($F(1,58)=0.53$, ns).

Rate of extruding. Experimental males extruded the tongue at a significantly greater rate than did controls (Condition: $F(1,232)=20.57$, $P<0.01$) and the interaction between pen and condition was a significant one ($F(3,232)=$

3.71, $P<0.05$). An analysis of the simple main effects showed significant increases in the adult female's pen ($F(1,58)=9.34$, $P<0.01$), in the pen housing two juveniles ($F(1,58)=5.25$, $P<0.05$), and in the single juvenile's pen ($F(1,58)=7.43$, $P<0.01$). (See Table 31.) The rates of tongue extruding in the empty pen were similar in the two conditions, however ($F(1,58)=1.00$, ns). The significant pen effect found in terms of the number of extrusions performed was not present when the data were analyzed in terms of the rate of extruding (Pen: $F(3,232)=2.56$, ns).

Marking. As in Experiment 1, experimental males showed a clear increase over the control males in the number of total marking behaviors. Unlike the previous fall, however, this increase was not limited to the pen housing the adult female.

Both the difference between control and experimental total marking behaviors and the interaction between pen and condition were significant (Pen: $F(3,232)=2.25$, ns; Condition: $F(1,232)=4.47$, $P<0.05$; Interaction: $F(3,232)=3.06$, $P<0.05$). However, an analysis of simple main effects showed only the changes in the pen inhabited by the single juvenile female to be statistically significant ($F(1,58)=4.04$, $P<0.05$). Nevertheless, as Table 32 illustrates, a distinct increase in total marking behaviors also occurred in the adult female's home area.

While more experimental males (12) marked than did

Table 31. Mean Number of Tongue Extrusions Performed Per Minute in Each of the Four Pens. Males, Experiment 3.

	Pen 1 (Empty Pen)	Pen 2 (Two Juvenile Females)	Pen 3 (One Juvenile Female)	Pen 4 (Adult Female)
Control (n=30)	.26 ± .19	.19 ± .16	.25 ± .22	.19 ± .09
Experimental (n=30)	.30 ± .17	.31 ± .22	.44 ± .31	.61 ± .76

Note: Pens are designated by experimental resident animals for the sake of clarity. All pens were empty in the control condition.

Table 32. Total Marking Behaviors Performed in Each of the Four Pens: Defecations (DEF), Pelvic Rubs (PR), and Chin Wipes (CW). Males, Experiment 3

	Pen 1 (Empty Pen)			Pen 2 (Two Juvenile Females)			Pen 3 (One Juvenile Female)			Pen 4 (Adult Female)		
	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW	DEF	PR	CW
Control (n=30)	2	3	0	3	1	0	1	1	1	0	0	0
Experimental (n=30)	0	0	0	1	0	1	3	26	2	1	15	1

Note: Pens are designated by experimental resident animals for the sake of clarity. All pens were empty in the control condition.

controls (7), this increase was not significant ($X^2(1)$= 1.93, ns).

When the three types of marking behaviors are examined separately, it becomes apparent that they were not of equal importance. Similar to the results of the previous fall, the marking results of this experiment provide no evidence that chin wipes were involved in the depositing of chemicals (Pen: $F(3,232)=1.28$, ns; Condition: $F(1,232)=1.83$, ns; Interaction: $F(3,232)=0.20$, ns). Although defecations seemed an important source of chemicals in Experiment 1, this was not the case in this experiment (Pen: $F(3,232)=0.86$, ns; Condition: $F(1,232)=0.10$, ns; Interaction: $F(3,232)=1.62$, ns).

The critical marking behavior in Experiment 3 was undoubtedly pelvic rubbing. While only five pelvic rubs were demonstrated by control males, experimental males performed 41 rubs, a significant increase ($F(1,232)=4.51$, $P<0.05$). Neither the pen effect nor, more important, the interaction between pen and condition were significant (Pen: $F(3,232)=2.02$, ns; Interaction: $F(3,232)=2.49$, ns).

Nevertheless, experimental males were probably responding to some factor or set of factors in terms of the particular pens they chose as rubbing sites. As Table 32 illustrates, control males distributed their pelvic rubs more or less equally among the four pens. Experimental males, on the other hand, performed all 41 pelvic rubs

either in the pen housing the adult female or in the single juvenile female's area. Contrary to what might be expected, the increase in pelvic rubbing was greater in the single juvenile's pen than in the pen inhabited by the adult female. If the data are adjusted, however, to take into account the time each subject spent per pen, the rate of rubbing is slightly higher in the adult female's pen (0.09 rubs/min) than in the single juvenile's area (0.06 rubs/min).

Seconds spent bobbing. While experimental males spent more time performing bobbing displays than did controls (see Table 33), the difference between the two groups was not statistically significant. In addition, no significant pen effect nor interaction between pen and condition occurred in terms of the total bobbing seconds performed (Pen: $F(3,232)=1.20$, ns; Condition: $F(1,232)=0.33$, ns; Interaction: $F(3,232)=2.61$, ns). (See Table 34).

As in the case of total bobbing, the number of seconds spent bobbing in conjunction with tongue extrusions increased in the experimental condition. Again, however, neither the main effects nor the interaction were significant (Pen: $F(3,232)=1.05$, ns; Condition: $F(1,232)=2.57$, ns; Interaction: $F(3,232)=1.71$, ns).

Number of pens entered. Experimental males entered a mean number of 2.3 pens, significantly more ($t(58)=2.19$, $P<0.05$) than the mean number entered by controls (1.8 pens).

Table 33. Mean Seconds Spent Bobbing and Mean Seconds Bobbing In Association With Tongue Extrusions. Males, Experiment 3.

	Seconds Spent Bobbing	Seconds Bobbing In Association With Tongue Extrusions
Control (n=30)	9.5 ± 14.6	1.4 ± 2.4
Experimental (n=30)	11.5 ± 12.7	2.9 ± 4.2

Table 34. Mean Total Seconds Spent Bobbing and Mean Seconds Bobbing in Association with Tongue Extrusions in Each of the Four Pens.
Males, Experiment 3.

	Pen 1 (Empty Pen)	Pen 2 (Two Juvenile Females)	Pen 3 (One Juvenile Female)	Pen 4 (Adult Female)
TOTAL BOBBING				
Control (n=30)	3.9 ± 12.2	1.9 ± 3.6	2.4 ± 4.6	1.3 ± 4.3
Experimental (n=30)	0.4 ± 1.5	4.0 ± 8.3	5.2 ± 9.1	1.9 ± 4.2
BOBBING WITH TONGUE EXTRUSIONS				
Control (n=30)	0.5 ± 2.1	0.3 ± 0.7	0.6 ± 1.4	0.1 ± 0.5
Experimental (n=30)	0.0 ± 0.0	1.1 ± 3.0	1.0 ± 1.9	0.8 ± 2.4

Note: Pens are designated by experimental resident animals for the sake of clarity. All pens were empty in the control condition.

Pen entered first. Experimental males entered Pen 4 (adult female) first more often than did controls and entered Pen 1 (empty) first less often than did controls (see Table 35). There was little difference between control and experimental subjects in the number of times they entered Pen 2 (two juvenile females) and Pen 3 (one juvenile female) first. Differences between groups were not significant, however ($X^2(3)=5.47$, ns).

Like control males the previous year, both control and experimental males in Experiment 3 entered Pen 2 first most frequently.

Intra-group comparisons. As in Experiment 1, the data were analyzed for intra-group differences in tongue extrusions performed and time spent per pen so that the two breeding seasons might be compared.

A two-way ANOVA showed no significant differences in the number of tongue extrusions performed by the first and second halves of the control group ($F(1,112)=2.01$, ns) and no significant interaction between group and pen ($F(3,112)=0.86$, ns). Unlike the previous year, there was no significant pen effect ($F(3,112)=1.50$, ns). An analysis of the time spent also showed no significant main effects (Pen: $F(3,112)=1.51$, ns; Group: $F(1,112)=0.00$, ns) and no significant interaction ($F(3,112)=1.29$, ns).

A two-way ANOVA showed no significant differences in the number of tongue extrusions performed by the two ex-

Table 35. Release Procedure and Initial Pen Preference. Males, Experiment 3.

	Release Procedure*		First Pen Entered	
	Observer Exited	Subject Facing	Number of Control Subjects Entering Pen First	Number of Experimental Subjects Entering Pen First
Pen 1	7	8	8	3
Pen 2	8	7	13	11
Pen 3	8	7	7	9
Pen 4	7	8	2	7

*Control and Experimental Conditions Were Identical.

perimental halves ($F(1,112)=0.25$, ns) and no significant interaction between group and pen ($F(3,112)=1.21$, ns). There was, however, a significant pen effect ($F(3,112)=5.69$, $P<0.01$), although no one pen was found to be significantly different from the other three. A two-way ANOVA of the time spent showed the same significant pen effect ($F(3,112)=4.45$, $P<0.01$), again with no one pen being significantly different from the other three. There was no significant group effect ($F(1,112)=0.00$, ns) and no significant interaction between group and pen ($F(3,112)=1.04$, ns).

Summary of Male Responses. Table 36, presenting the mean performances of male subjects in Experiment 3, has been included for easy comparison with the responses demonstrated by males in Experiment 1 (Table 16) and Experiment 2 (Table 29).

Discussion

As might be expected, the data indicate that breeding males have more difficulty in discriminating between the chemicals deposited by juvenile and adult females than in differentiating between the chemical deposits of adult males and adult females. Nevertheless, there is evidence that breeding males can differentiate between mature and immature females on the basis of chemicals deposited and are attracted to an area containing the deposits of the adult female.

Table 36. Tongue Extrusions, Marking, and Time Spent Bobbing by Male Subjects (Mean±SD). Experiment 3.

	MALES
Tongue Extrusions	
Control (n=30)	6.7 ± 6.2
Experimental (n=30)	10.6 ± 7.8
Seconds Spent Bobbing	
Control (n=30)	9.5 ± 14.6
Experimental (n=30)	11.5 ± 12.7
Seconds Bobbing In Association With Tongue Extrusions	
Control (n=30)	1.4 ± 2.4
Experimental (n=30)	2.9 ± 4.2
Marking (All Categories)	
Control (n=30)	0.4 ± 0.8
Experimental (n=30)	1.7 ± 3.1
Pelvic Rubs	
Control (n=30)	0.2 ± 0.4
Experimental (n=30)	1.4 ± 3.0

There was a significant increase in the number of tongue extrusions performed in the adult female's pen, while increases in the two areas housing juvenile females were not significant. In addition, the data concerning the distribution of time among the four pens show trends which generally support the conclusion that males are able to distinguish between the chemicals of juvenile and adult females and are attracted to the area containing the latter. The data concerning the time spent in each pen are somewhat complicated, however, by a significant pen effect indicating that some factor(s) other than the chemicals present in each area contributed to the relative attractiveness of the four pens.

The results of Experiment 3 again point strongly to pelvic rubbing as a means by which breeding males deposit chemicals and thus suggest that the femoral pores and/or the cloaca produce chemicals important in mating. Unlike the previous fall, however, the results of this experiment do not implicate defecations as a source of male chemicals. It should be noted, however, that while subjects can perform chin wipes and pelvic rubs at will, there is a natural limit to the number of defecations they can produce in any given time period. Because of this possible ceiling effect, defecations should not be rejected as a means of depositing chemical signals.

The placement of total marking behaviors and, more

important, of pelvic rubs among the four pens is somewhat puzzling. While the increase in the number of pelvic rubs in Experiment 1 occurred only in the adult female's pen, this was not the case in Experiment 3. In this experiment, although a substantial increase occurred in the pen inhabited by the adult female, there was an even greater increase in the number of pelvic rubs performed in the single juvenile's home area.[1] Assuming on the basis of the tongue extrusion data that males could determine where the adult female resided and preferred her area, there are two possible explanations for the greater number of pelvic rubs performed in the juvenile's pen: (1) Pelvic rubbing is a general response to heightened sexual arousal and is not place-specific. (2) The pen areas were artificial both in terms of size and sharpness of boundaries. Subjects may have had more difficulty determining the boundaries in Experiment 3 than in Experiment 1.

The first possibility, that once aroused males are indiscriminate in where they perform pelvic rubs, seems unlikely. Increases in pelvic rubbing were clearly limited to one pen in Experiment 1 and to two pens in Experiment 3. Several factors, however, point to the second possibility. The areas inhabited by the resident animals

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[1] The increase in the rate of rubbing was slightly greater in the adult female's pen, however.

differed from natural territories in that they ended abruptly rather than gradually. In a natural setting, a male could detect the chemicals left by a female, move a foot or two away and rub his pelvis, and still be within the female's home range. This would not necessarily be the case in the experimental condition where a male could detect a female's chemicals near the boundary between two pens, move a short distance away to rub, and be in an area never frequented by the female. In Experiment 1, it may have been clearer to males exactly when they were leaving the adult female's area, as her pen was bordered by the adult male's pen on one side and the empty pen on the other (see Figure 1). In Experiment 3, the adult female's pen was bordered by the single juvenile's pen and the empty pen (see Figure 2). It may have been more difficult for males to determine exactly where the adult female's area ended when it was bordered by a space occupied by another female. Since the total number of pelvic rubs performed was relatively small, a few errors in making this discrimination would have had a disproportionate effect on the overall distribution of rubs among the four pens. Tongue extrusions, on the other hand, were performed far more frequently and by more individuals than were pelvic rubs. Thus, occasional errors in detecting this boundary would have had a minimal effect on the overall results.

Finally, there is again no evidence that S. jarrovi respond with visual displays to chemicals deposited by conspecifics.

CHAPTER VI

SUMMARY AND COMPARISON OF THE THREE EXPERIMENTS

Males

In both breeding seasons (Tables 37 and 39), there was a significant interaction between the number of tongue extrusions performed in each pen and the treatment condition. In Experiment 1, this interaction seemed to result from an increase in extrusions performed in the adult female's pen and a decrease in the number performed in the adult male's area, while in Experiment 3, the interaction resulted from a significant increase performed in the adult female's pen and a significant decrease in the empty pen. In Experiment 3, experimental males also performed significantly more tongue extrusions than did controls.

When the tongue extrusion data are analyzed in terms of the rate of extruding, Experiments 1 and 3 both showed significant increases in the performance of experimental males as compared to controls and significant interactions between pen and condition. In Experiment 1, this interaction was due to significant increases in the rate of extruding in both the adult female's pen and the juvenile male's pen, while the interaction in Experiment 3 resulted from significant increases in the rates of extruding in all three areas housing females. In interpreting the rate data, however, it's important to remember that the group mean for the appropriate treatment condition was substi-

tuted for those situations in which a subject did not enter a particular pen and thus had no rate score. As these mean scores comprised half the raw data, this reduced enormously the high variability characteristic of S. jarrovi behavior, thus not only making statistical significance much easier to achieve but also rendering a rather artificial picture of the subjects' performance.

In both breeding seasons, experimental males showed significant increases in the number of marking behaviors performed as compared to controls (see Tables 37 and 39). In addition, the number of individuals involved in marking was significantly greater in the experimental condition of Experiment 1 than in the control condition. In both Experiments 1 and 3, there was a significant interaction between marking behaviors performed in each pen and treatment condition. In Experiment 1, this interaction resulted from an increase in marking in the adult female's pen. The interaction in Experiment 3 was due to a significant increase in the single juvenile female's area, although a substantial increase also occurred in the pen housing the adult female.

Experimental and control males also demonstrated significant differences in both breeding seasons in terms of pelvic rubs performed. In Experiment 1, the number of individuals involved in pelvic rubbing increased significantly in the experimental condition. In Experiment 3, experi-

mental males performed a significantly greater number of pelvic rubs than did controls, and this increase was limited to the pen in which the adult female resided and to the pen housing the single juvenile female.

Both the number of defecations performed and the number of individuals defecating were significantly greater in the experimental condition of Experiment 1 than in the control condition. No similar differences were noted in Experiment 3, however.

The data obtained during the non-breeding months (Table 38) are interesting in the lack of significant differences shown between experimental and control males.[1] The significant interaction between pen and condition in terms of tongue extruding found during both breeding seasons was not seen in the spring. Moreover, there was a total absence of pelvic rubbing in the spring months compared to the significant increases in this behavior seen during both breeding seasons.

Females

There were no significant differences between experimental and control females in either Experiment 1 or Experiment 2 (Tables 37 and 38) to indicate that females might respond to the chemical deposits of conspecifics.[1]

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[1] The significant decreases in behaviors performed by experimental subjects as compared to controls in Experiment 2 appear to have been a function of high temperatures requiring the animals to seek shelter.

Males vs. Females

There were no significant differences between males and females during the spring months. During the breeding season, however, males in both treatment conditions performed significantly more tongue extrusions than did females (Table 37).

Table 37. Summary of Significant Results: Experiment 1.

MALES					
Tongue Extrusions:	Number Behaviors	Interaction	P<0.05	↑ Adult♀ Pen ↓ Adult♂ Pen	
	Rate	Interaction	P<0.05	↑ Adult♀ Pen ↑ Juv. ♂ Pen	P<0.05 P<0.01
		Exp. > Control	P<0.05		
Combined Marking:	Number Behaviors	Interaction	P<0.05	↑ Adult♀ Pen	
		Exp. > Control	P<0.05		
	Individuals Involved	Exp. > Control	P<0.025		
Pelvic Rubs:	Individuals Involved	Exp. > Control	P<0.01		
Defecations:	Number Behaviors	Exp. > Control	P<0.05		
	Individuals Involved	Exp. > Control	P<0.025		
FEMALES					
No significant differences between control and experimental groups were found.					
MALES VS. FEMALES					
Tongue Extrusions:	Number Behaviors				
	Control	Males > Females	P<0.05		
	Experimental	Males > Females	P<0.01		

Table 38. Summary of Significant Results: Experiment 2.

MALES			
Seconds Spent Bobbing:		Exp. < Control	P<0.05
FEMALES			
Tongue Extrusions:	Number	Exp. < Control	P<0.05
	Rate	Exp. < Control	P<0.01
Seconds Spent Bobbing:		Exp. < Control	P<0.05
MALES VS. FEMALES			
No significant differences between males and females were found.			

Note: All differences noted above pertain to behaviors only. No significant differences were found in terms of numbers of individuals involved.

Table 39. Summary of Significant Results: Experiment 3.

MALES					
Time Spent in Each Pen:		Pen Effect	P<0.05	↑1 Juv.♀ Pen	
Tongue Extrusions:	Number	Interaction	P<0.01	↑ Adult♀ Pen ↓ Empty Pen	P<0.01 P<0.05
		Pen Effect	P<0.05		
		Exp. > Control	P<0.05		
	Rate:	Interaction	P<0.05	↑ Adult♀ Pen ↑1 Juv.♀ Pen ↑2 Juv.♀♀ Pen	P<0.01 P<0.01 P<0.05
		Exp. > Control	P<0.01		
Combined Marking:		Interaction	P<0.05	↑1 Juv.♀ Pen ↑ Adult♀ Pen	P<0.05
		Exp. > Control	P<0.05		
Pelvic Rubs:		Exp. > Control	P<0.05	↑ Adult♀ Pen ↑1 Juv.♀ Pen	
Number of Pens Entered:		Exp. > Control	P<0.05		

Note: All differences noted above pertain to behaviors only. No significant differences were found in terms of number of individuals involved.

CHAPTER VII

CONCLUSIONS

When the three experiments are examined together, it becomes clear that male Sceloporus jarrovi utilize chemicals in mating. Specifically, the experiments show that breeding males can detect the chemicals deposited by adult females and are attracted to areas containing these deposits over empty areas and over areas containing chemicals deposited by juvenile females or by other males. The data also illustrate the importance of pelvic rubbing as a means by which breeding males deposit chemicals. These results point to the femoral pores as at least one source of these chemicals, although substances from the cloacal region could also be deposited by rubbing the pelvis on the substrate.

The data are less clear as to whether males use chemical signals in the maintenance of territories. There is some evidence that breeding males detect the chemicals deposited by other adult males in the fall and that they avoid areas containing these chemicals. No similar evidence was found during the spring months, however.

Evidence for the detection of chemical signals by female S. jarrovi is much weaker. While the data hint that females may respond to the deposits of conspecifics during the breeding season, there is no such indication

for the spring months.

An interesting question raised by these findings involves the function of the chemicals deposited by males during the breeding season. Are these deposits signals to other males, to females, or to both sexes? As males focus their pelvic rubbing in highly desirable areas (i.e. those inhabited by adult females), chemicals deposited in this manner could serve as territorial markers excluding other breeding males from the rubbing sites. On the other hand, the fact that pelvic rubbing occurs in areas inhabited by adult females could, of course, indicate that the deposits are signals to breeding females. Since females generally make only small shifts in their territories after establishing them early in the year, it is unlikely that male chemicals function to attract females to sites that they don't already frequent. Perhaps male chemicals serve instead as a primer for females in a role analogous to, and complementary with, that of courtship displays. It is also possible that a single chemical deposited by pelvic rubbing could affect males and females differentially or that more than one chemical might be deposited through pelvic rubbing.

Although these experiments demonstrate the presence of female chemical signals and point to at least one of the functions they serve (attracting males), the data unfortunately shed no light on the source of these chemicals

or on how they are deposited.

An important area not dealt with in these experiments concerns the interaction between the vomeronasal and olfactory systems in saurian communication. Since the vomeronasal organ responds to most of the chemicals which activate olfactory receptors (Burghardt, 1980), we would certainly expect there to be some such interaction. In at least one study using skinks (Duvall et al, 1980), subjects responded to air-borne chemicals originating from conspecifics, further indicating that olfaction may play some part in chemical communication. Cowles and Phelan (1958) suggest that olfaction is a low-discrimination/high-sensitivity system which operates independently of the vomeronasal system, probably serving to activate further lingual exploration. If, as Burghardt (1980) concludes, the squamate vomeronasal system is generally a high-discrimination system specialized for low-volatility, proximal stimuli, then the two chemical senses appear to complement each other. In this interaction, it seems that the olfactory system functions to detect air-born, distal stimuli, thus bringing the animal into physical contact with chemicals which are then analyzed by the more precise vomeronasal system (see Duvall, 1980). In any respect, the interaction of the two chemical systems in mediating the social behavior of lizards warrants further investigation.

Although the focus of this study was necessarily limited to chemical communication, it is important to remember that chemical signaling does not occur in a vacuum divorced from other modes of intra-specific communication or from other life-sustaining, non-communicatory behaviors. S. jarrovi are, after all, primarily visual animals, with an extensive and well-documented repertoire of visual displays involving structures specialized for communication in both their color and form. In fact, visual displaying in iguanid species in general is so prominent a behavior that only recently have we become aware that these animals may utilize communication systems based on other modalities as well.

As visual and chemical systems serve several overlapping functions for a number of species, it is reasonable to assume that they may interact. This could occur in any number of ways: chemical signals may trigger visual displaying, as suggested by Duvall (1979); visual displays may be responded to by the depositing of chemicals; behaviors involved in the depositing of chemicals, such as pelvic rubbing, may become incorporated in displays; and, finally, the chemicals themselves, when in the form of fecal pellets or visible smears, may serve as visual signs in addition to conveying chemical information.

Considering the general reliance of S. jarrovi upon vision, the overlap found between visual and chemical signals in mediating mating, and the positive results obtained by Duvall (1979) with a closely related species, it is curious that no evidence for an interaction between the two communication systems was found in this study. This may be due more to the differences between field and laboratory techniques than to any differences between the two species. In Duvall's laboratory study the stimulus used was purposely saturated with chemicals, while in the three experiments presented here chemicals were distributed over a large area in concentrations approximating those found in the subjects' natural habitat. Perhaps the supra-normal stimulus used by Duvall elicited an unusually strong response, compared to more subtle responses in the field situation which may have occurred but at levels too low for statistical significance.

Communicatory behaviors in general, regardless of the sensory modality involved, must also be seen in the larger context of all behaviors potentially beneficial to the individual at any given time and place. Subjects in the experiments presented here were confronted with an unfamiliar, complex situation and were permitted a wide range of responses. Among other things, they had to thermoregulate, watch for predators, and obtain food. To varying degrees, potential responses to the chemical deposits of conspeci-

fics may have been rejected in favor of competing behaviors more necessary to the animal's immediate well-being.

Behaviors are multiply-determined, not only by the requirements of the individual but by features of the environment. The chemical deposits of conspecifics were only one of many such features. Wind direction, thermogradients, and visual aspects of the area may have exerted important influences on both the sensory information subjects received and the responses they made to that information. These variables and/or the fact that S. jarrovi are visually dominant may have been responsible for the pen effects found in which some unknown factor(s) over-rode the effect of resident chemical deposits.

In contrast to field experiments, the environment in laboratory studies is typically stripped of all variables except the one being examined and subjects are limited in the types of responses they are able to make. With the environmental stimuli reduced and fewer competing behaviors possible, one might expect a stronger than usual response to the few variables present. While laboratory studies are effective in uncovering subtle responses which can be missed in the field, field experiments are valuable in establishing the relative importance of the response in the larger context of the ani-

mal's "everyday" experience and in understanding the features of the environment which help to shape the behavior in question. Rather than concluding that the interaction of visual and chemical communication is markedly different in S. jarrovi and S. occidentalis (the species used by Duvall), it is probably more likely that the results of the two studies reflect two sides of the same coin and should be interpreted together.

The series of experiments presented here raises a number of questions for further research. Replications of Experiment 1, preferably with larger sample sizes, would help in clarifying whether breeding males respond to the deposits of other adult males and in determining whether breeding females respond to the deposits of either sex. Related to this is the question of the function(s) of the chemicals deposited by pelvic rubbing, particularly in terms of their possible priming effect on females. An area completely beyond the scope of this study, but certainly of interest, concerns the composition and production of the chemicals involved in communication. Finally, the specific functions served by chemical communication in various saurian groups and the interaction of chemical communication with systems based on other modalities are intriguing areas which have only recently received the attention they deserve.

The study presented here barely scratches the sur-

face of saurian chemical communication. By pointing out the use of both chemical and visual signals by S. jarrovi, however, it does illustrate the richness and complexity possible in saurian social interactions and challenges the stereotype of lizards as possessing only limited behavioral flexibility.

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