

AN ABSTRACT OF THE THESIS OF

Carol E. Bickford for the degree of Master of Science
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Title: Aspects of the Social Structure of the California Ground
Squirrel (*Spermophilus beecheyi*) in Western Oregon

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Bruce E. Coblentz

A population of *Spermophilus beecheyi* was studied to determine patterns of individual spacing, behavioral interactions among different sex and age classes, and the relationship between aspects of *S. beecheyi* social structure and sociality to those of other sciurids. Research was conducted on a population of squirrels living in an abandoned rock quarry on Finley National Wildlife Refuge near Corvallis, Oregon. Squirrels were trapped, marked with dye, and observed during March through October, 1977, and March, 1978. The location of each squirrel and the type and location of any encounters were recorded during 325 hours of observation.

The types of encounters most often observed were approach/withdrawal, greeting/investigation, play, displacement, aggression, and the male-initiated paw push. The two major activity peaks occurred in March, corresponding to courtship activity and male defense of breeding territories, and in July, corresponding to the activity of juveniles. The seasonal activity cycle of *S. beecheyi* had five phases: breeding, pre-emergence of young, litter, pre-hibernation, and hibernation. No distinct time of dispersal was determined.

The population consisted of approximately twice as many adult females as adult males. Both sexes had overlapping home ranges, but their centers of activity were usually separate from the activity centers of other members of the same sex. Home ranges were retained from year to year by the same squirrel.

The most social sciurids are those which exhibit a high frequency of cohesive behaviors, such as greeting and mutual grooming. The S. beecheyi at Finley National Wildlife Refuge tended to be tolerant of other individuals, but did not maintain a high level of cohesive behavior within the population. The social structure of S. beecheyi was intermediate to the more social S. columbianus and the more solitary S. franklinii.

Aspects of the Social Structure of the
California Ground Squirrel (Spermophilus beecheyi)
in Western Oregon

by

Carol E. Bickford

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APPROVED:

Redacted for Privacy

Assistant Professor of Wildlife Ecology
Department of Fisheries and Wildlife
in charge of major

Redacted for Privacy

Chairman of Department of General Science

Redacted for Privacy

Dean of Graduate School

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Typed by Carol E. Bickford for Carol E. Bickford

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I dedicate this paper to Critter the coyote and the experiences which guided my interest in animal behavior. I also dedicate this thesis to the three squirrels which died during two seasons of trapping at Pigeon Butte and, especially, to adult female 131, who died in a trap on July 3, 1977.

I wish to thank Doc Storm for aiming me in the right direction, Leona Nicholson for encouraging me to reapply to the General Science Department, Dennis McDonald for supporting me as his graduate student and research assistant, and Bruce Coblenz both for rescuing me during my search for a new major professor and for his understanding and valuable advice throughout the writing of my thesis. I also thank the other members of my examining committee for their suggestions: Larry Forslund, Frank Moore, and Cliff Michel. I am grateful for the privilege of using part of Finley National Wildlife Refuge for my study area, and I thank the staff for their cooperation. Lastly, I wish to express my love and appreciation to my parents and friends for their understanding and support.

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Aspects of the Social Structure of the California
Ground Squirrel (Spermophilus beecheyi) in Western Oregon

The social system of a species both integrates individual and group behaviors and regulates population dispersion. Integration and regulation arise through interaction and communication among members of a population. These processes result in social structure, the patterns of individual spacing and relationships among individuals. Traditional studies of social structure describe species characteristics in terms of seasonal changes in type and frequency of interactions, interactions among animals of different age classes and sexes, the structure and stability of the family group, spacing of individual or group home ranges, and the nature of dominance hierarchies or territoriality (Dunford, 1977a).

Research has been conducted on the social systems of several sciurids. One of the earliest and now classic works on sciurid social behavior was King's (1955) study of black-tailed prairie dogs (Cynomys ludovicianus). Barash (1974) and Armitage (1975, 1977) studied social systems within the genus Marmota. Several researchers have observed social behavior within the genus Spermophilus. In particular, Steiner (1970, 1972, 1974) and Michener (1973, 1974, 1977) extensively studied Columbian (Spermophilus columbianus) and Richardson's (Spermophilus richardsoni) ground squirrels. Kivett, Murie, and Steiner (1976) compared scent-marking methods of some spermophiles, and suggested that with increasing sociality, the amount of scent-marking behavior increased and the type of scent marking became more elaborate.

Three basic aspects of species sociality are: a/ the composition and stability of the family group; b/ the nature of individual spacing within the population; and, c/ the types and frequency of cohesive behavior within the population.

a/ Composition and stability of the family group

The stability of the family group varies with the lengths of the male/female and mother/young bonds, as well as with the onset of dispersal (Crook, Ellis, and Goss-Custard, 1976). Dunford (1977a) suggested two general trends in the evolutionary transition from the less complex kin clusters to the more complex social groups of some sciurids: an increased role for the male in the family group and longer retention of offspring within the mother's home range. Family group size among squirrel species varies from the single mother/young unit to the harem containing one or two males, several females, and offspring up to 2 years old; the length of the male/female bond ranges correspondingly from a few hours to an entire active season.

King (1955) found that black-tailed prairie dogs (C. ludovicianus) were highly social and lived in coterie containing one to two adult males with several adult females and young. The areas in which these harems lived were defended against non-members, especially by the dominant male; this male also initiated much of the greeting behavior within the coterie. Dispersal was delayed for at least one year after birth (King, 1955). In contrast, white-tailed prairie dogs (C. leucurus) lived in family groups headed by the female parent (Tileston and Lechleitner, 1966).

Among marmots, the Olympic marmot (Marmota olympus) and the hoary marmot (Marmota caligata) were the most social and lived in colonies composed of male and female adults, two year olds, yearlings, and young of the year (Barash, 1974). Dispersal occurred among two year olds and breeding was delayed until three years of age. Yellow-bellied marmots (Marmota flaviventris) also lived in colonies, but were less social. Dispersal occurred among yearlings, and breeding was delayed until two years of age (Barash, 1974). Woodchucks (Marmota monax) were the least social marmots, lived solitarily, and dispersed as juveniles (Barash, 1974). Because M. olympus and M. caligata inhabited alpine meadows, M. flaviventris lived in rocky areas at intermediate elevations, and M. monax inhabited woodland/field ecotones at low elevations, Barash (1974) suggested that marmot sociality was related to the length of the growing season in a particular habitat. He theorized that the harsher the environment inhabited by a certain marmot species, the greater the species' tendencies toward late dispersal, late maturation, slow recruitment, social tolerance, and colonial organization. Armitage (1977), however, found that dispersal times still differed for M. flaviventris and M. olympus populations that lived where growing seasons were the same length, and that the growth rates of juvenile M. flaviventris were significantly greater at a high elevation colony than at a lower elevation colony.

Kivett, et al. (1976) suggested that environmental harshness might explain the range of sociality among spermophiles: adaptation to high altitudes or high latitudes might result in sufficient family or group cohesion to allow delayed sexual maturation and delayed

dispersal of young. They reported that S. columbianus inhabited medium to high elevations, lived in groups with one territorial adult male, one or more adult females, yearlings, and young of the year; yearlings dispersed but did not breed until the following year. According to the environmental harshness theory, Arctic ground squirrels (Spermophilus undulatus) should have a social structure similar to that of S. columbianus. Kivett, et al. (1976) observed that the social characteristics of S. undulatus appeared to be like that of the Columbian ground squirrel. Dispersal, however, occurred among juvenile S. undulatus between 8 and 10 weeks old (Carl, 1971).

Among other spermophiles, the basic social unit was mother and young, the mother/young bond was shorter than in S. undulatus and S. columbianus, and yearlings were included in the breeding population (Kivett, et al., 1976). The length of the mother/young bond ranged from 6-7 weeks in the California ground squirrel (Spermophilus beecheyi; Tomich, 1962) down to 12-14 days in the thirteen-lined ground squirrel (Spermophilus tridecemlineatus; McCarley, 1966). Round-tailed ground squirrels (Spermophilus tereticaudus) juveniles remained in their mother's home range for up to 6 weeks (Dunford, 1977b). Juvenile Belding's ground squirrels (Spermophilus beldingi) and juvenile Townsend's ground squirrels (Spermophilus townsendii) dispersed 4-6 weeks after weaning (Turner, 1972; Johnson and Melquist, 1975), while juvenile Richardson's ground squirrels (S. richardsoni) remained within their mother's home range for the first 3-4 weeks after emergence (Michener and Michener, 1977). Franklin's ground

squirrel (S. franklinii) exhibited little maternal care aboveground and, after 2-3 weeks, adults sometimes attacked and chased young (Balph, 1963).

Although there are typically more females than males in spermophile spring populations, the sex ratio of juveniles at birth is unity (Dunford, 1977b). Reasons postulated for the change in sex ratio are the dispersal of juvenile males, predation, and differential mortality related to hibernation (Michener and Michener, 1977). Michener and Michener (1977) found that although dispersal accounted for some loss of juvenile male S. richardsoni, most of the loss occurred between September and the following spring. Other than dispersal, they suggested: 1/ that mortality could occur during the 2-3 weeks prior to hibernation when only juvenile males were active aboveground; 2/ that juvenile males had the last choice of hibernation burrows and these might not be suitable for overwinter survival; 3/ that cannibalism could occur if males hibernated in the same burrow; and 4/ that males were more subject to harsh environmental conditions because they emerged from hibernation earlier than females (Michener and Michener, 1977).

In several spermophiles, juvenile females remain within their mother's home range. As Michener and Michener stated (1973), the year-to-year retention of a home range by a female or her female offspring insures the use of areas that have already been proven adequate for reproduction and hibernation. S. richardsoni females shared overlapping home ranges with their adult female offspring; overcrowding may have been prevented by the up to 60% between-year losses of juvenile females (Michener and Michener, 1977). Female

young of S. beldingi used those portions of their mother's home range which were not extensively used by their mother or other juveniles (Turner, 1962). Dunford (1977a) found that female S. tereticaudus established territories adjacent to those of other sibling females and in the same general area as their mother's territory.

b/ Individual spacing within the population

Individuals or family groups may maintain territories or freely interact with other individuals or groups. Territories may be maintained permanently or temporarily. No distinct social hierarchy existed within a C. ludovicianus coterie, except for dominance of one male during the breeding season. The area of the coterie was freely accessible to all members, but was defended against non-members (King, 1955). C. leucurus did not defend a family group area and sometimes shared feeding grounds with other family groups (Tileston and Lechleitner, 1966).

M. olympus did not maintain territories or distinct home ranges, and all parts of the colony were equally accessible to all colony members (Barash, 1974). M. flaviventris lived in colonies but maintained individually distinct home ranges, and each individual maintained a large physical distance from other individuals (Barash, 1974). M. monax lived solitarily, maintaining dominant/subordinate relationships with neighbors (Bronson, 1964).

In S. columbianus, the dominant male defended the group area and its residents (Steiner, 1970). S. undulatus lived in either refugee colonies or breeding colonies. Two types of areas were defended within the breeding colony: in the spring, males defended

areas within which the females established burrows, and in the fall, each member of the population defended a territory prior to hibernation (Carl, 1971). In other spermophiles, home ranges overlapped extensively: S. richardsoni (Michener, 1973), the rock squirrel (Spermophilus variegatus; Stalheim, 1965), and S. armatus (Balph, 1963). Territoriality in these species was in defense of breeding territories and of burrows containing young. Michener (personal communication, 1979) observed that in the core area of its home range, an S. richardsoni individual was dominant to other squirrels. S. armatus and S. tridecemlineatus were intolerant of other squirrels within an individual distance (Balph, 1963; Wistrand, 1974).

c/ Cohesive and disruptive behaviors within the population

The type and frequency of interactions within a population reflects the degree of sociality of a species. Species of high sociality will exhibit a high frequency of cohesive behaviors, such as greeting, mutual grooming, and play; species of low sociality will exhibit disruptive behaviors in the form of mutual avoidance or a high frequency of agonistic encounters.

Greeting, allogrooming, and mutual burrow construction occurred frequently within a C. ludovicianus coterie (King, 1955), whereas greeting occurred infrequently and mutual grooming did not occur in C. leucurus (Tileston and Lechleitner, 1966). M. olympus exhibited a high frequency of greeting behavior (about one greeting per animal per hour) in the early morning, especially in the spring (Barash, 1974). Although mutual grooming occurred in M. flaviventris

(Armitage, 1975), greeting occurred infrequently (about one greeting per animal every 10 hours; Barash, 1974). Greeting behavior has not been described for M. monax (Barash, 1974), and individuals tended to avoid each other (Bronson, 1964). Among spermophiles, the range between high and low sociality is less distinct. Allogrooming has been reported in S. columbianus (Betts, 1976) and S. richardsoni (Yeaton, 1972). Greeting behavior occurred in most spermophiles, but was infrequent or absent in S. tridecemlineatus and S. franklinii (Wistrand, 1974; Kivett, et al., 1976).

Juvenile play has been reported in several sciurid species: the tassel-eared squirrel (Sciurus aberti; Farentinos, 1972), the gray squirrel (Sciurus carolinensis; Horwich, 1972), C. ludovicianus and C. leucurus (King, 1955; Tileston and Lechleitner, 1966), M. olympus (Barash, 1974), S. columbianus (Steiner, 1970), S. richardsoni (Yeaton, 1972), S. beldingi (Turner, 1972), S. variegatus (Stalheim, 1965), S. beecheyi (McDonald, 1977), and S. tridecemlineatus (McCarley, 1966).

Male aggression is common during the breeding season of sciurids. During a group chase, males of the tree squirrels S. carolinensis and S. aberti fought over access to the female (Taylor, 1966; Farentinos, 1972). Breeding territories were established via male aggression among S. columbianus and S. undulatus (Steiner, 1970; Carl, 1971), and springtime agonistic behavior was observed among S. armatus and S. tridecemlineatus males (Balph, 1963; Wistrand, 1974).

Female aggressiveness in sciurids is common prior to the emergence of young from the burrow. S. carolinensis females defended

their nest tree against other females (Taylor, 1966). Pregnant or lactating C. ludovicianus females were aggressive toward males and other females (King, 1955). Females of M. olympus, S. columbianus, S. richardsoni, and S. townsendii chased other squirrels away from their burrows (Steiner, 1970; Michener, 1973; Barash, 1974; Johnson and Melquist, 1975). Pregnant S. beldingi chased exploring males or non-neighboring females (Turner, 1972); Sherman (unpublished manuscript) observed that S. beldingi females were especially aggressive toward unrelated females. S. armatus and S. tereticaudus females became intolerant of other squirrels and somewhat dominant to males (Balph, 1963; Dunford, 1977b).

The period between litter break-up and hibernation is characterized by aggressive behavior in several sciurids. Adults chased young in C. leucurus (Tileston and Lechleitner, 1966), S. undulatus (Carl, 1971), and S. franklinii (Balph, 1963). The late spring or midsummer dispersal of young is often associated with increased aggression by adults, especially females, as occurred in M. monax (Barash, 1974), S. beldingi (Turner, 1962), S. tridecemlineatus (McCarley, 1966), S. townsendii (Johnson and Melquist, 1975), and S. tereticaudus (Dunford, 1977b).

Armitage (1975) theorized that the occurrence of dispersal and recruitment in marmots was not determined by population density, but by behavioral density, the number of aggressive or amicable behaviors which occurred within the population; the activity of one animal could therefore be responsible for a high encounter rate within the population (Armitage, 1977). Residency or dispersal of a potential

population recruit resulted from the interaction between the recruit's behaviors and the types and numbers of behaviors exhibited by the resident adults (Armitage, 1975). This theory could account for the dispersal of some juveniles and not others from spermophile populations as well as from marmot populations.

The California Ground Squirrel

Although the social structures of several spermophiles have been studied, little has been written regarding the social structure of the California ground squirrel, S. beecheyi. Early studies of S. beecheyi were carried out largely due to their classification as agricultural pests. Emphasis was usually on their life histories and on the most efficient means of killing them. One of the first descriptions of S. beecheyi was Grinnell and Dixon's (1918) account of the distribution and natural history of several subspecies. Edge (1931, 1934, 1935) described habitat, predators, burrows, seasonal activity and growth of S. beecheyi in western Oregon. Storer (1930) documented the occurrence of spring and late summer/early fall pregnancies; most authors recognize only a spring breeding season in S. beecheyi. Storer, Evans, and Palmer (1944) studied the home range and seasonal activity of this species.

Evans and Holdenried (1943) studied the natural history of S. beecheyi, including seasonal cycles, population composition, home range size, dispersal, and a brief account of social behavior. In his natural history classic The California Ground Squirrel, Linsdale (1946) described life history information and his observations of the squirrels. Because the observations were written in a narrative

account rather than tabulated as data, it is difficult to make generalizations from Linsdale's findings. Fitch (1948) studied the ecology of S. beecheyi and wrote a more general account than Linsdale's. Tomich's (1962) study of S. beecheyi's annual cycle emphasized physiological changes but included data on the seasonal variation in the age and sex composition of the populations he trapped.

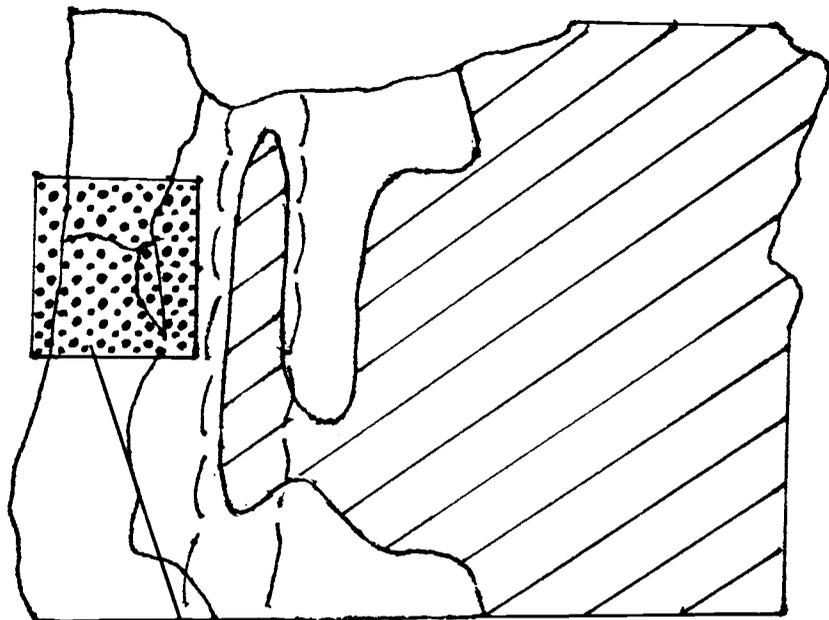
Hunt (1974, unpublished manuscript) studied three components of habitat selection in S. beecheyi: visibility of approaching predators, the distribution of forbs, and the distribution of burrows. Owings and Borchert (1975) also studied correlates of burrow location. More recently, Owings and Coss (1977) described the snake-mobbing behavior of this squirrel. McDonald (1977) studied the relationship between play and exercise in S. beecheyi. Owings, Borchert, and Ross (1977) conducted the only study dealing exclusively with the social behavior of S. beecheyi; however, this study was conducted only in the spring, when squirrel behavior is significantly altered by breeding and raising of young.

The objectives of my research were:

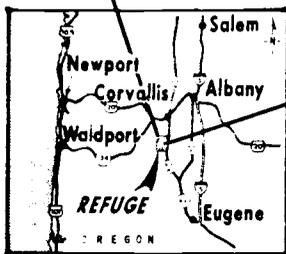
- 1/ to determine the patterns of individual spacing within a population of S. beecheyi.
- 2/ to describe behavioral interactions among S. beecheyi of different sex and age classes.
- 3/ to compare aspects of S. beecheyi social structure and sociality with those of other sciurids.

STUDY AREA

Research was conducted in an abandoned rock quarry at Pigeon Butte (T.13S., R.5W., S.32) on William L. Finley National Wildlife Refuge near Corvallis, Oregon (Figure 1). The 80 acre quarry (elevation 300-500 feet) faced SSE and was divided into three levels by two rocky slopes (Figure 2). Grasses and blackberries (Rubus procerus, R. laciniatus and R. pedatus) formed the majority of the vegetative cover; however, the slopes and most of the flat midlevel were free of vegetation. The upper level was covered with grasses and an oak forest (Quercus garryana), which was an important foraging area during the period of acorn availability.



RANGE OF S. BECHEYI IN OREGON



UNITED STATES DEPARTMENT OF THE INTERIOR
 FISH AND WILDLIFE SERVICE
WILLIAM L. FINLEY
NATIONAL WILDLIFE REFUGE
BASTON COUNTY, OREGON

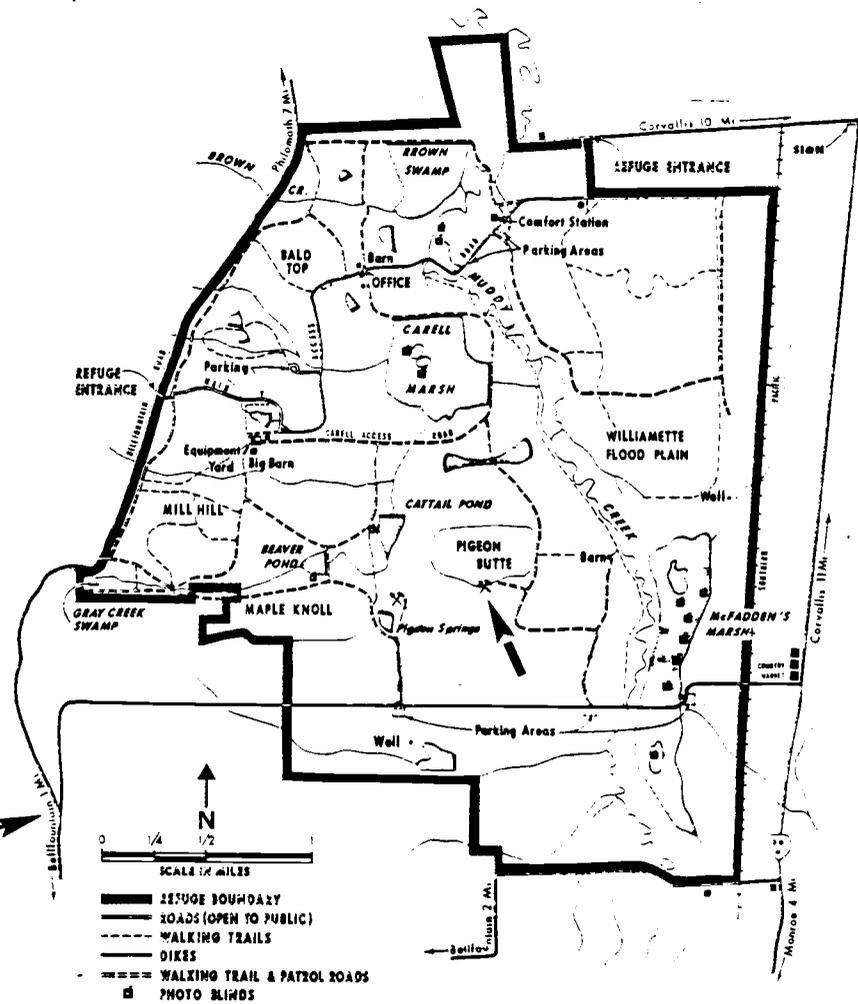


Figure 1. Location of study area at Pigeon Butte rock quarry on William L. Finley National Wildlife Refuge near Corvallis, Oregon.

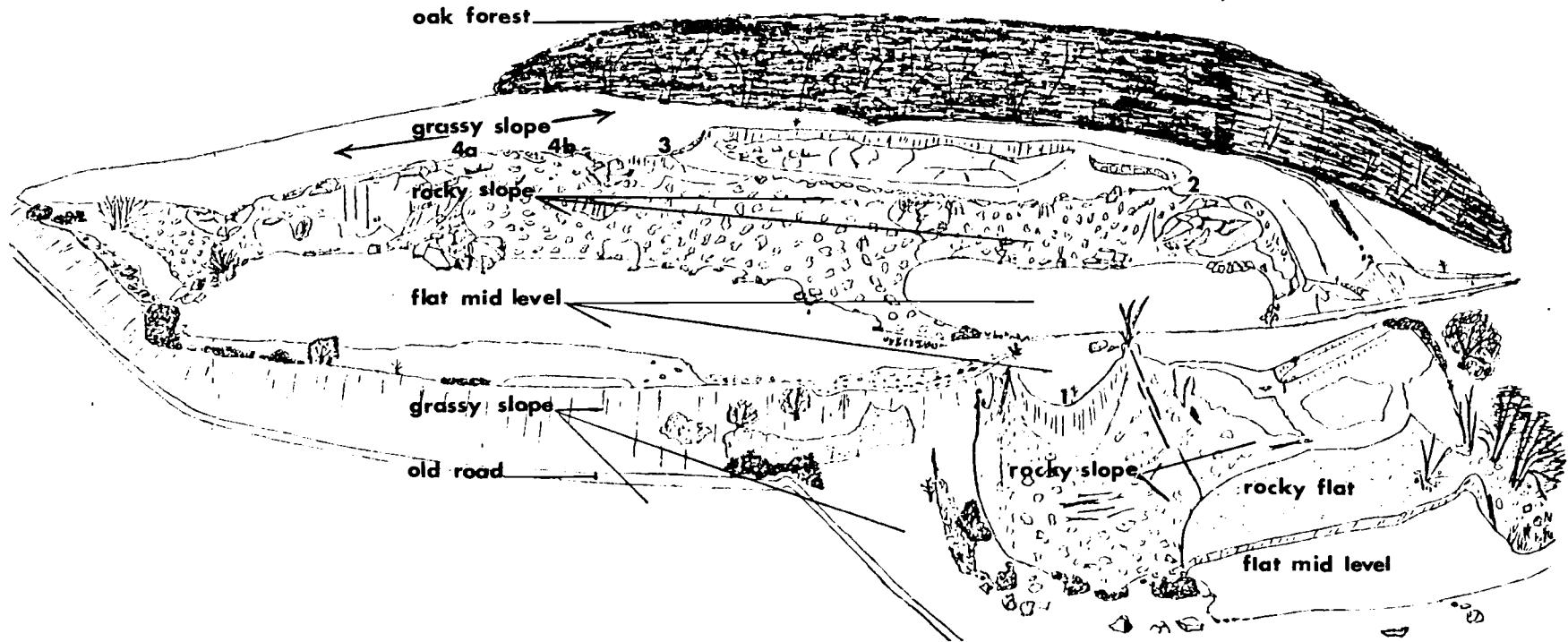
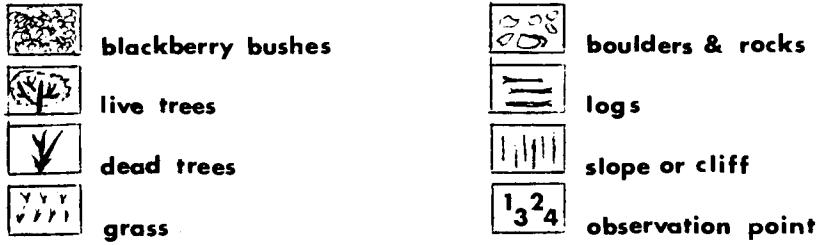


Figure 2. Map of Pigeon Butte rock quarry, Finley National Wildlife Refuge, near Corvallis, Oregon

METHODS

Research was conducted from 13 February to 23 October, 1977, and 10-21 March, 1978. Squirrels hibernated from November to January. Of the 95 days of research conducted in 1977, 38 days included trapping with Tomahawk live traps baited with peanut butter. Between 13 February and 7 September, 75 squirrels were captured, sexed, classified as adult or juvenile, and marked with Jamar D cattle fur dye, using a handling device (Emlen, 1944). Each squirrel was marked with its own distinctive pattern and assigned a number. Due to complete fading of the marks on some squirrels, a few were probably assigned more than one number and marking.

On each day, observations of marked and unmarked squirrels were made from the same four vantage points in the quarry. Daily observation time was divided equally among the vantage points, and each observation point was visited in a different sequence from that of the previous day. Each section of the quarry was assigned a number which I used to record a particular squirrel's location. The location, type of encounter, time of occurrence, and participants of the encounter were also recorded. Encounters were classified as greeting/investigation, aggression, approach/withdrawal, displacement, follow, courtship, and play. The identity and location of squirrels performing the cheek rub, twist mark and dirt-bathing motions were recorded, as were the time of day and number of times each motion was performed.

The frequencies with which encounter types were performed throughout the season were compared on the basis of encounter rates, the number of encounters seen per hour of observation. The monthly

encounter rate for each type of encounter was graphed to show changes in encounter rates through the season. Daily encounter rates were graphed for March, 1978.

To aid in mapping of individual home ranges, a detailed map of the study area was made (Figure 2). Black and white pictures of the quarry were overlapped and traced; the traced drawings were then reduced. The home range for each squirrel was determined by plotting on the map each sighting and capture of that squirrel. For each ten minute interval that the squirrel remained at a particular location, another point was plotted on the map; areas where the squirrel spent more time were thereby easier to detect. The points were plotted directly onto the map, while the home range lines were drawn on tracing paper held over the map. Monthly home ranges were drawn for each squirrel by delineating the area containing the plotted points. The yearly home range of each squirrel was plotted separately from a composite of all of its monthly home ranges. The area where 3 monthly home ranges overlapped was designated the core area (Kaufmann, 1962 from Dunford, 1977a); where 4 or more monthly home ranges overlapped was designated the home core area. The yearly home ranges and core areas of each sex were then grouped on a composite map to determine the degree of home range/core area overlap.

BEHAVIORAL DESCRIPTIONS

The encounter types observed in this study were categorized as greeting/investigation, approach/withdrawal, displacement, aggression, courtship, play and follow. Approach/withdrawal described the encounter type in which one squirrel approached another and then moved away. Displacement, which was considered an aggressive behavior, occurred when one squirrel approached another and the other moved away. Greeting sometimes occurred between approach and withdrawal of either squirrel. Greeting involved two squirrels sniffing each other's nasal or cheek areas, whereas investigation involved one squirrel sniffing another's nose, cheek, body or anogenital area. Play encounters between juveniles included paw pushing, boxing, pounces, mounts, chases, lateral curves and wrestling. "Follow" described the behavior of one squirrel following, not chasing, another at a distance of 5-25 feet.

Aggression occurred when one squirrel chased or fought with another. Aggression by adult females involved a high intensity chase and sometimes lunges at the retreator's rear. Male aggressive encounters involved chases throughout the year, but included fighting in the spring. When a male saw another male in his breeding territory, he approached rapidly and chased the other male out of the area. If the other male did not retreat, there was a standoff in which both males stood side-to-side and sometimes head-to-tail in what McDonald (personal communication) termed a "lateral-curve" posture (Figure 3). Often the squirrels fluffed their fur and stood on their toes, possibly to look larger. From the lateral curve posture the squirrels would begin pushing against each other with their shoulder or flank

area (Owings, Borchert, and Ross: Figure 6). When one squirrel was knocked offbalance, he could retreat or fight. A fight ensued when one or both squirrels pounced upon each other and became a mass of biting, kicking bodies. Another standoff might then follow, or one male might retreat with the other in close pursuit; a chase might be interrupted with several standoffs. The fighting resulted in injuries such as torn ears and gashes in the back, belly and head regions. S. undulatus (Carl, 1971), S. columbianus (Betts, 1976), and S. tridecemlineatus (Wistrand, 1974) males performed aggressive behaviors similar to those described for S. beecheyi males.

Courtship activity began with an approach by the male and his performance of a paw push (MPP) upon the female (Figure 4). The MPP consisted of the male tapping the female's right forelimb or shoulder repeatedly with his right forepaw and then tapping her left forelimb or shoulder repeatedly with his left forepaw; these movements were also initiated with the left forepaw to left foreleg. Meanwhile the male's head was held back and his eyes partially closed. After the MPP was performed one or more times, the female might then turn her rear toward the male and raise her tail (TRRT), allowing him to sniff her anogenital area (Figure 5). (TRRT followed MPP 29 out of 69 times that MPP was performed.) After the rear sniff by the male, the female moved 2-5 feet and again paused in the TRRT position; the male followed and again sniffed her. This procedure might be repeated several times before one participant left or both moved out of sight. Because MPP and TRRT were also observed outside of any apparent sexual context, the category of courtship encounters was divided into

MPP and TRRT encounter types. TRRT appeared to be used as a form of submission in encounters seen in the field and, especially, in captivity.

Courtship most often began with an MPP, but rapid chases by the male were observed. Such chasing behavior is typical of other sciurid species: S. variegatus (Stalheim, 1965), S. tridecemlineatus (McCarley, 1966; Wistrand, 1972), S. armatus (Balph, 1963), S. aberti (Farentinos, 1972), and S. carolinensis (Horwich, 1972; Thompson, 1977). The MPP may function in appeasement of a defensive female. Initially, the S. carolinensis female responded to the breeding male with defensive attacks, and the male exhibited approach/withdrawal responses (Horwich, 1972). S. armatus males had both a rapid and slow approach to the female. If the male approached too rapidly, he was threatened, bitten, or chased by the female; if he approached slowly with his eyes partially closed, the female did not threaten or bite him, and a mating chase followed. Balph (1963) interpreted this slow approach as appeasement of the female. Both S. beecheyi and the closely related rock squirrel (S. variegatus) performed sexual trailing combined with MPP's. Stalheim's description (1965) of S. variegatus courtship closely corresponded to my observation of the courtship of S. beecheyi.

Possible scent-marking behaviors of S. beecheyi were the cheek rub, twist mark, and dirt-bathing motions. The cheek rub involved a tilting and forward thrust of the head such that the mouth-corner gland was rubbed against the substrate. Twist marking was a forward spiral movement that resulted in the top of the head and dorsal glands being rubbed against the substrate (Kivett, et al., 1976). These

movements are pictured for S. columbianus in Steiner (1974: Figures 1-3). Sometimes S. beecheyi rubbed only the top of the head or shoulder against the substrate. The dirt-bathing motions were similar to those pictured in Steiner (1974: Figure 7). S. undulatus, S. richardsoni, and S. lateralis performed similar marking behaviors (Kivett, et al., 1976); these species and S. columbianus had oral scent glands, located at the mouth corner, and dorsal scent glands, located in species-specific patterns along the back (Kivett, et al., 1976). Linsdale (1946) found such dorsal glands in S. beecheyi.

Although dirt bathing and twist marking have not been proven to serve scent-marking functions, the areas in which these behaviors were performed received considerable olfactory attention from both the performers and other squirrels. Squirrels interrupted their twist marking to sniff the substrate against which they were rubbing. Out of 217 observations of scent-marking behaviors, 43 were performed when a squirrel appeared to be upset, either after release from a trap (7 observations) or after an encounter with another squirrel (36 observations). Marking was also seen in conjunction with a stereotyped grooming of the cheeks, nose and tail (12 observations).

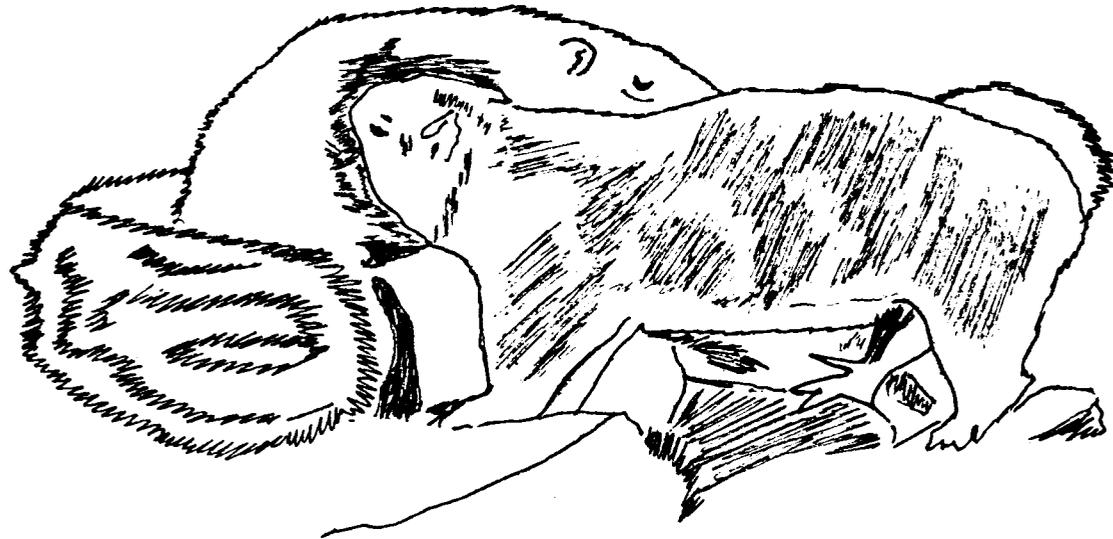
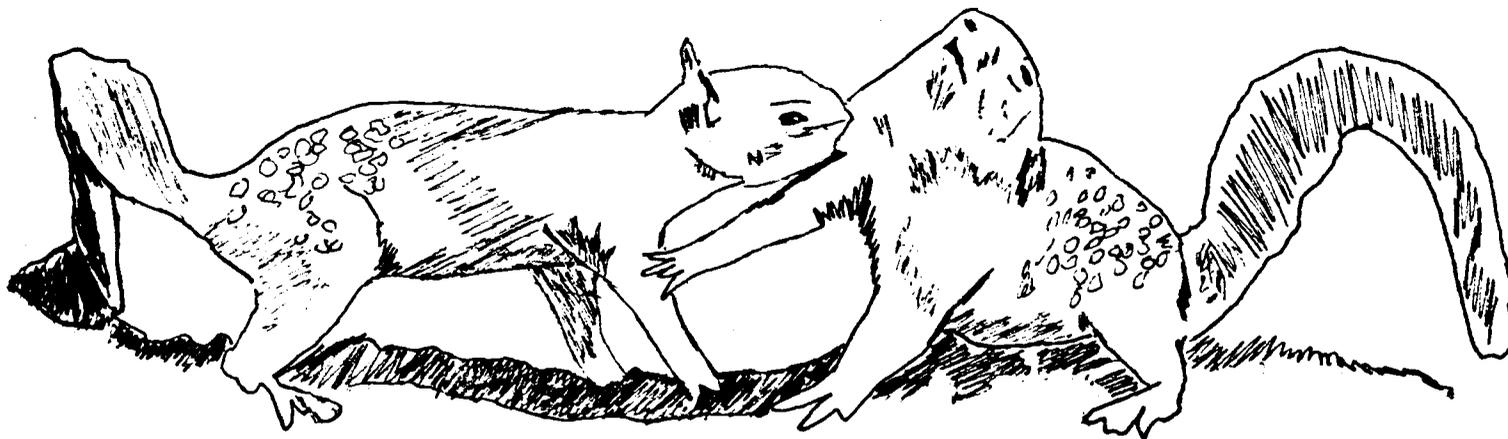
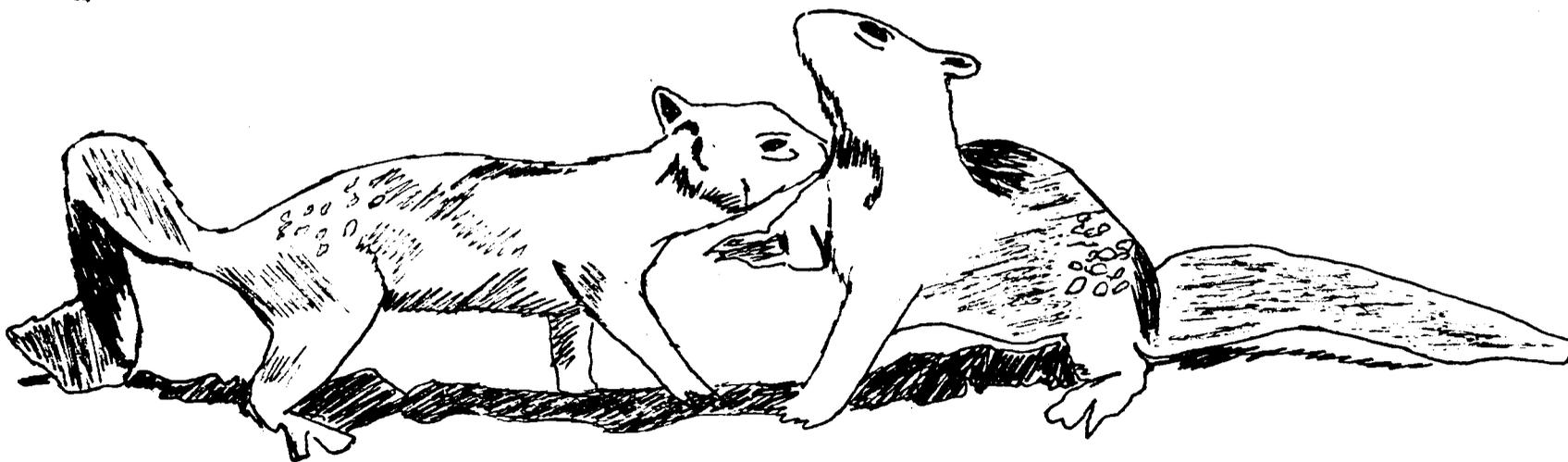


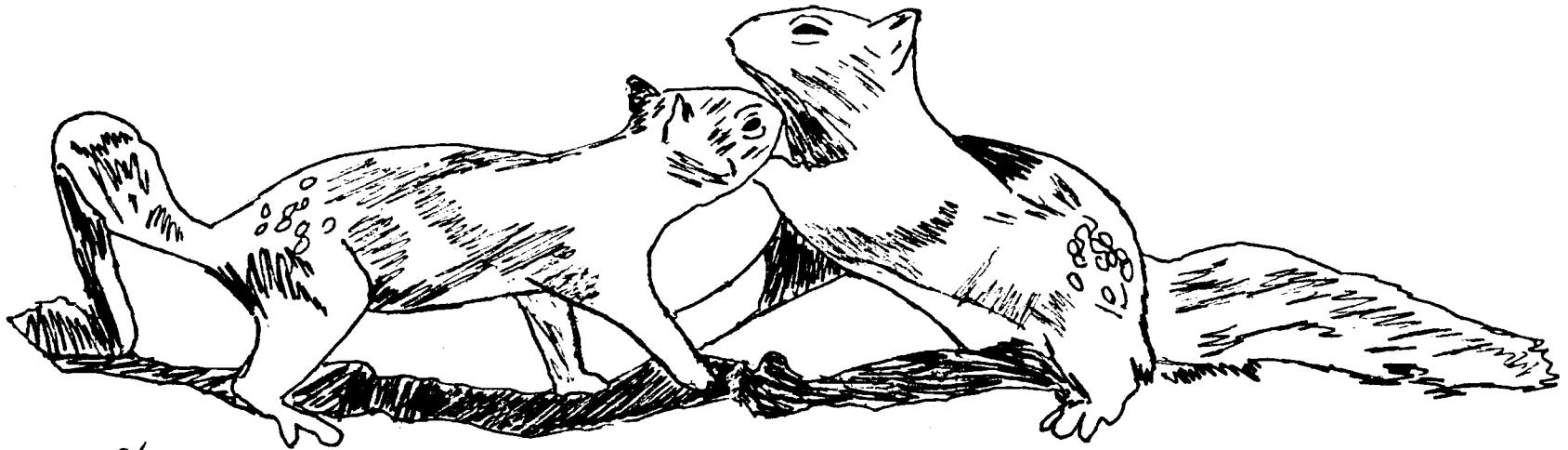
Figure 3. Aggressive lateral-curve posture between adult male S. beecheyi drawn from 16mm film taken during July, 1976 at Pigeon Eutte, Finley NWR.



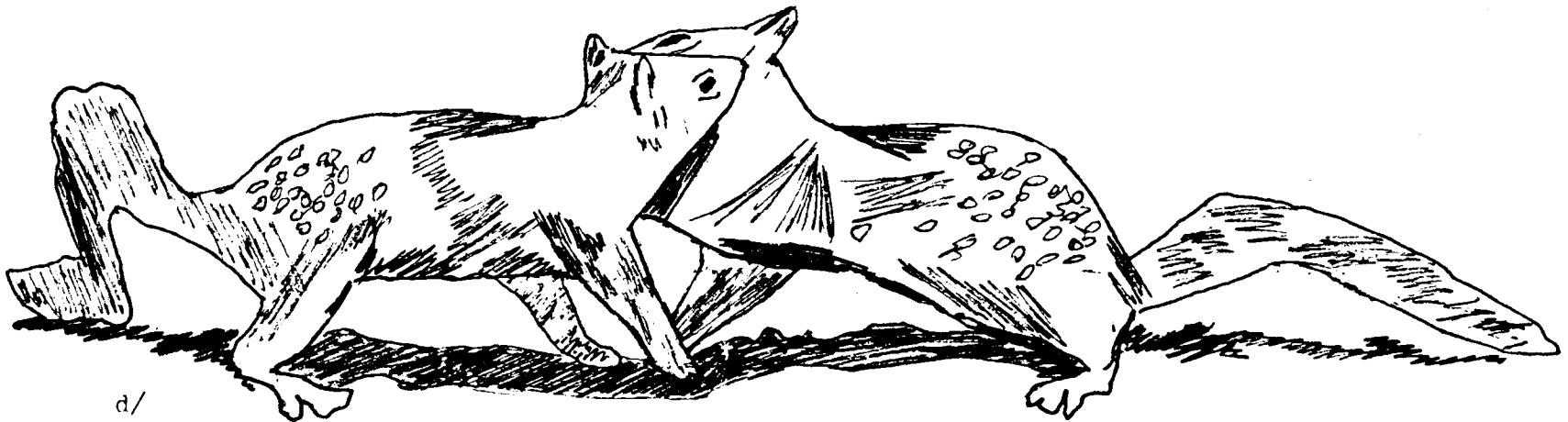
a/



b/ Figure 4. Male paw push (MPP) sequence between S. beecheyi drawn from 16mm film taken during the summer of 1976 at Pigeon Butte, Finley NWR. a/ shows male pushing with right forepaw against right foreleg of female; b/, 21 frames later, shows male beginning to switch forepaws.



c/



d/

Figure 4, continued. c/, 2 film frames after b/, shows male continuing to switch forepaws; and d/, 4 frames later, shows male pushing with left forepaw against left foreleg of female. Female withdrew 11 frames later.

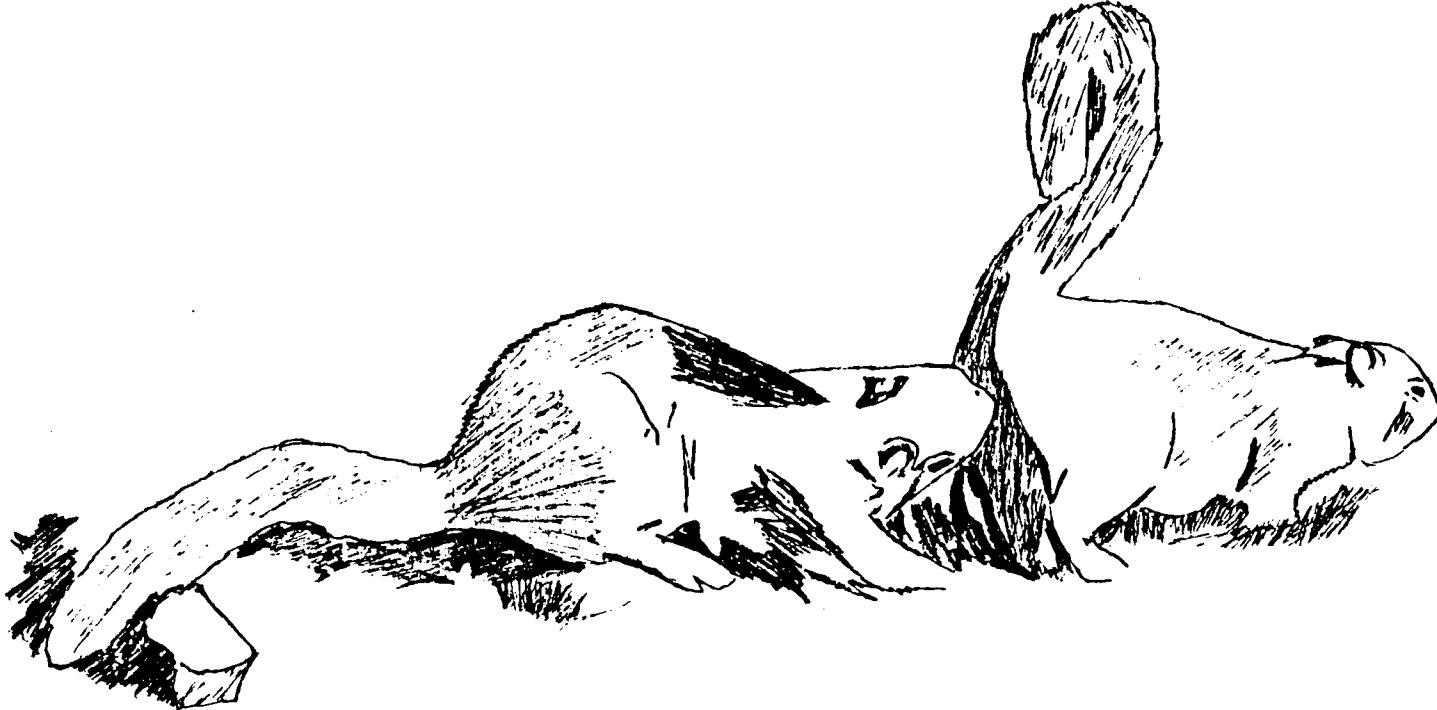


Figure 5. Investigative rear sniff by male and turn-rear-raise-tail position (TRRT) of S. beecheyi drawn from 16mm film taken during the summer of 1976 at Pigeon Butte, Finley NWR. Rear sniff and TRRT typically followed MPP during courtship, but were also seen in other contexts.

RESULTS

Between 13 February and 7 September, 1977, 75 squirrels were captured: 17 adult males, 35 adult females, 15 juvenile males, 7 juvenile females, and 1 juvenile whose sex was unknown. Between 15 March and 2 October, 1977, 34 squirrels were recaptured from 1-30 times. The readiness with which marked squirrels entered the traps made capture of additional unmarked squirrels difficult. Most of the juveniles were marked before their first molt and therefore lost their marks by June; only 2 juvenile males and 2 juvenile females retained their marks long enough to provide home range data through 1977.

In March, 1978, 3 adult males, 6 adult females, 2 yearling males, and 1 yearling female had retained their marks from 1977. Two other adult males were unmarked but recognizable, and one unmarked female was captured and marked. In total, 15 squirrels were identifiable during the March, 1978 observation period. All of the previously marked squirrels remained within their 1977 home ranges, although a few ventured somewhat further into adjacent areas. Part, if not all, of each squirrel's 1977 core area was included in its 1978 home range.

Home ranges were widely overlapping (Figures 6 and 7). Female home ranges overlapped more extensively than did those of males, and female core areas frequently overlapped. The separation of home core area from core area proved to be unnecessary for females, because females used their entire core area for more than 3 months. The known burrows in which young were raised were within the female's core area. Although 4 males had partially overlapping core areas, only 2 had home core areas which slightly overlapped. Whereas adult male yearly home

ranges overlapped with from 1 to 5 other adult male home ranges, they overlapped with 6 to 10 adult female home ranges. All but 1 male core area overlapped with at least 2 female core areas. Adequate 1977 and 1978 home range data was available for only 1 juvenile male and 1 juvenile female. The juvenile female's 1977 core area overlapped with those of 3 adult females, and her March, 1978 home range overlapped with those of 2 older females. The juvenile male's 1977 core area and 1978 home range overlapped with those of 2 older males. Because overlap in space is not equivalent to overlap in time, there was more individual separation than the home range maps might imply.

The paired t-test (Petersen, 1973) was utilized to test for association between encounters and encounter site; it was found that an encounter was as likely to be observed anywhere in a squirrel's home range as in its core area ($p > 0.10$). However, more encounters occurred per unit area of core area than per unit area of home range. The implication is that more encounters occurred within a squirrel's core area because the squirrel spent more time there.

Contingency tables (Siegel, 1956) were constructed for Chi square analysis to determine whether any marked squirrel participated in or won a significantly different number or type of encounter than any other squirrel in its sex and age class. For most squirrels, Chi square tests could not be performed due to an insufficient number (less than 5) in one cell of the contingency table. Where Chi square tests were performed, no differences were found in the amount of a squirrel's participation in encounters ($p > 0.10$, d.f.=1).

Seasonal Trends

The seasonal fluctuation in squirrel numbers seen per hour of observation is shown in Figure 8. Squirrel observations were somewhat higher than is shown for March and April of 1977 because not all unidentified squirrels were counted during those months. The overall encounter rate for 1977 was 273 encounters in 302.50 hours of observation, or 0.90 encounters per hour. July (1.3 encounters per hour) had the highest monthly encounter rate for 1977, largely due to the activities of juveniles. Fewer squirrels were observed in March and July, 1977, than in months with lower encounter rates, indicating that encounter rates were not simply artifacts of changing population density. The March, 1977 encounter rate was 1.2 in comparison to a higher March, 1978 rate of 4.6 encounters per hour of observation. The discrepancy between the March, 1977 and 1978 rates can be explained by the fact that more squirrel observations were recorded in 1978 (263 squirrels in 23.75 hours of observation) and by the differences in the dates during which observations were made (Table 1). The majority of the March, 1977 observations were made late in the month (22, 24-27 March), whereas the 1978 observations were made in mid-March (10, 12, 16-21), implying that breeding activities occur synchronously over a short period of time in mid-March.

Figure 9 shows that the majority of encounters during the March, 1978 breeding season were aggression, following, and male paw pushing (MPP). Some approach/withdrawals, greeting/investigation, and displacement occurred. The number of each type of encounter per day and the number of observations per day is shown in Table 1. Male

aggression was in the form of long, intensive chases, which were frequently interrupted by lateral curves and fights. Males chased any males found within their territory; at territorial boundaries the role of aggressor was exchanged between males, resulting in seesaw chases between neighbors. Following and MPP's were performed by males during courtship; however, males followed other males 3 out of 16 times. Aggression and MPP's accounted for most of the March, 1977 encounters.

Figures 10-16 show the seasonal trends in types of encounters throughout 1977. Table 2 shows the number of each type of encounter per month and the number of observations per month. The combination of all encounter types resulted in 2 activity peaks (Figure 10). The first peak occurred in March and corresponded to sexual activity and male territorial defense. The encounter rate fell to a low level in April, but began to climb again in May with the emergence of young. The second encounter rate peak occurred in July and was largely due to the activity of juveniles (Figure 11). Play was a juvenile activity, lasting from late May (May 21st) to mid-July (July 15th); play peaked in June at 0.47 encounters per hour of observation, when 24 play encounters were observed. Greeting/investigation also peaked in June (11 encounters) due to a juvenile either greeting an adult (4 encounters) or greeting another juvenile prior to play (7 encounters). TRRT was performed by some juveniles which had been approached by an adult or another juvenile (6 observations); either squirrel withdrew from the encounter. Approach/withdrawals and "following" were primarily juvenile activities.

Unlike the more juvenile encounter types, aggression, displacement and male paw pushing occurred throughout the seasonal activity cycle (Figure 12). There were 2 main peaks in MPP encounter rates; the first was due to the spring courtship activity of adult males (11 encounters), and the second to the activity of juvenile males (8 encounters; Figure 13). The aggressive encounter rate was analyzed according to the sex and age class of the aggressor (Figure 14). The adult male aggressive rate peaked during the March period of territorial defense (12 encounters in March, 1977), while the adult female rate climbed through the summer to a peak in August (4 encounters). Male-initiated aggression rose slightly in May (3 encounters) and in September/October (3 encounters), partly due to chases of unmarked squirrels. Adult female aggression (Figure 16a) was directed against both male and female adults from late pregnancy until after the emergence of young aboveground (10 encounters). After early June, most aggression by adult females was directed toward juveniles.

As the overall aggressive encounter rate declined, the overall displacement rate rose (Figure 15). Over the whole season, adult males displaced unmarked squirrels 12 times. Eight of these displacements occurred in late summer and early fall; however, the October peak occurred over a 3-4 day period between an adult male/unmarked female pair at one particular location in the quarry. The May-July displacement by juveniles was associated with play soliciting: a juvenile approached another playfully and the other juvenile left. The adult female displacement encounter rate is presented in Figure 16b. Adult females displaced adult males only 3 times during the

entire season. Adult females were displaced by other females 6 times, 4 of which occurred during the period of pregnancy and emergence of the young. During the July peak, adult females displaced 6 juveniles, 5 of which were female. A comparison of Figures 16a and 16b indicates that the peaks of aggression (10 encounters) and displacement (13 encounters) by adult females occurred in July and August. Aggression and displacement were directed toward juveniles (12 encounters), unmarked squirrels (6 encounters), other adult females (3 encounters), and adult males (2 encounters). Adult females displaced juvenile females five times and chased them only once. Adult females chased juvenile males twice but were not observed displacing juvenile males.

Preliminary data recorded in August, 1976 showed an encounter rate of 3.13 encounters per hour in contrast to the August, 1977 encounter rate of 1.17. The encounter types contributing most to this difference were aggression and the encounter types most typical of juveniles: play, greeting/investigation, approach/withdrawal and "follow". In 1977, these juvenile activities reached their peaks in June and July; play was not observed after mid-July. The lower 1977 encounter rate was probably due to the fact that 1977 was a hot drought year; squirrels tended to be relatively inactive during hot weather.

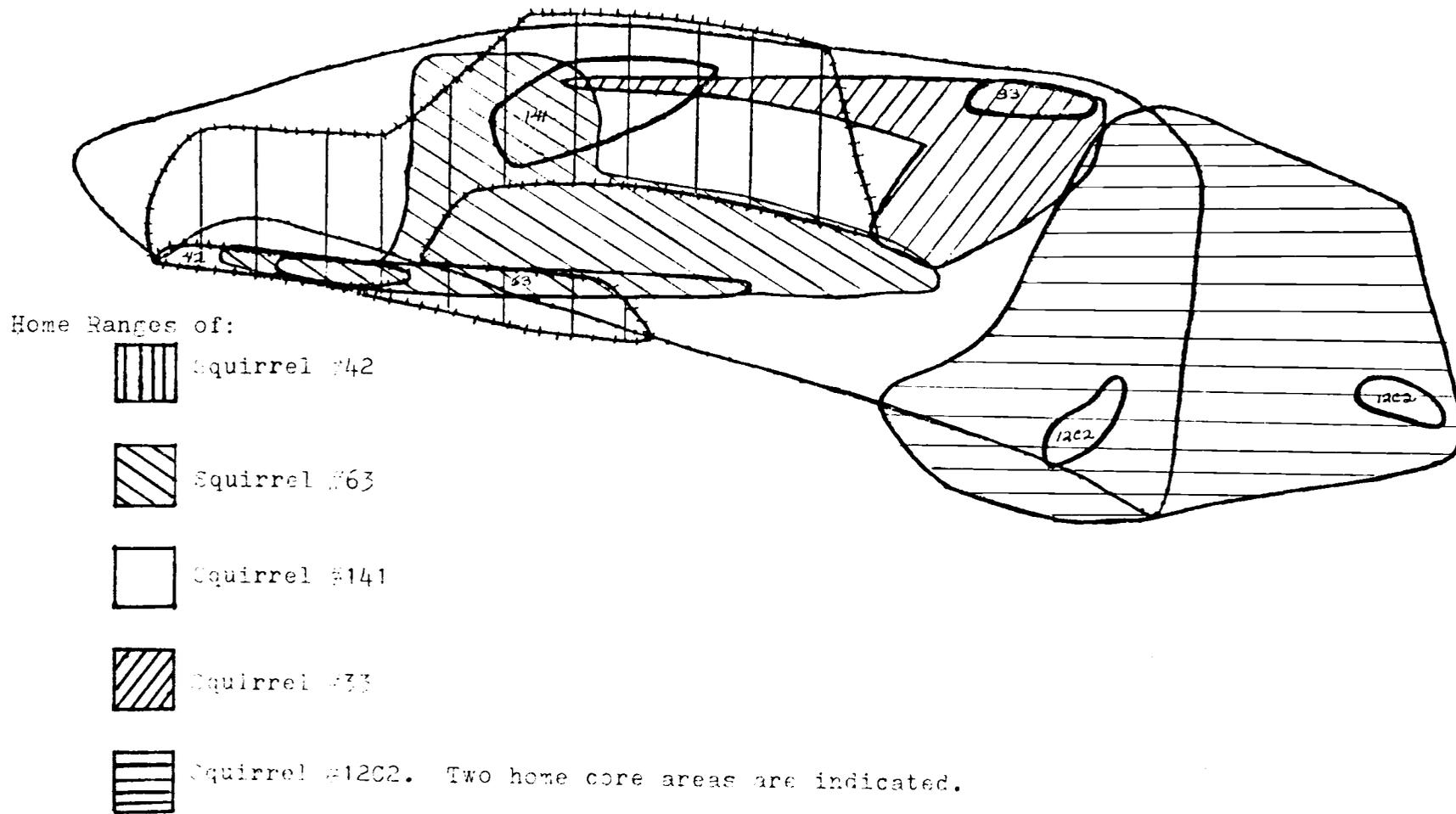


Figure 6. Overlap of the home ranges and home core areas of adult male *S. beecheyi* at Pigeon butte in 1977. Numbers indicate an individual male and are within that male's home core area.

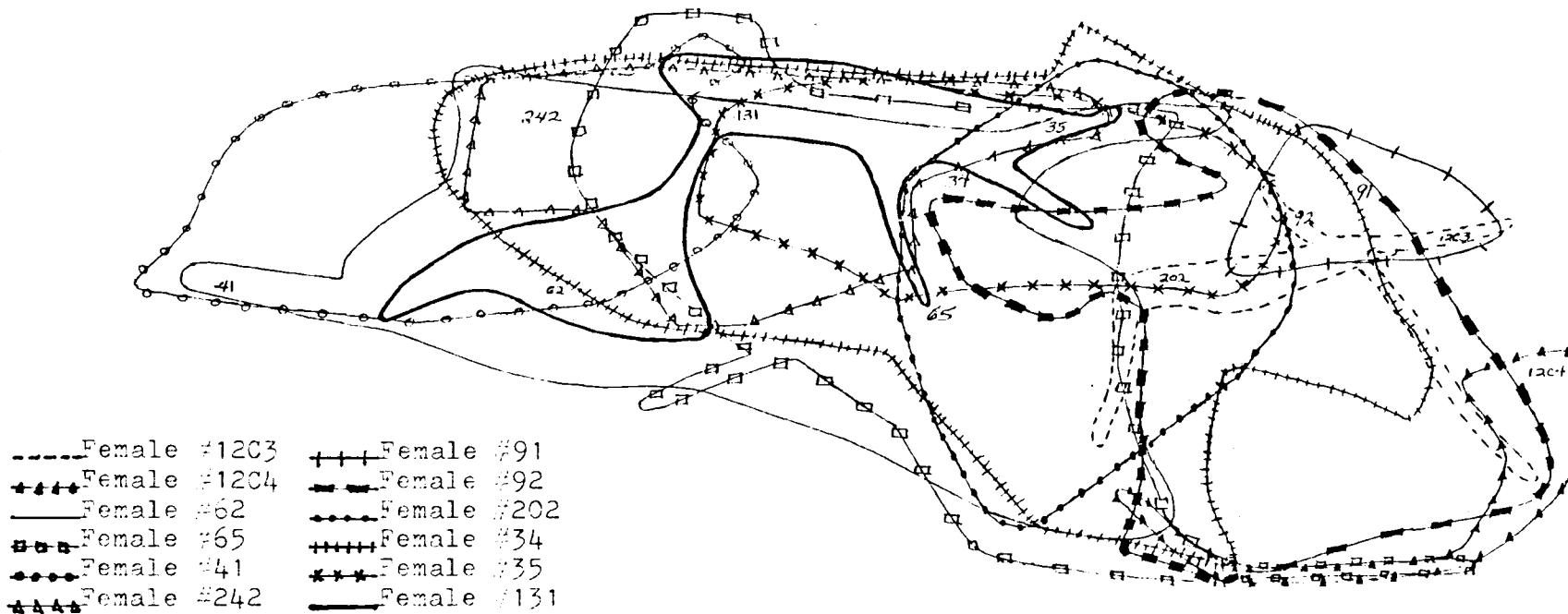


Figure 7a. Overlay of the home ranges of adult female *S. beccheyi* at Pigeon Butte in 1977. Numbers indicate an individual female and are within that female's home core area.

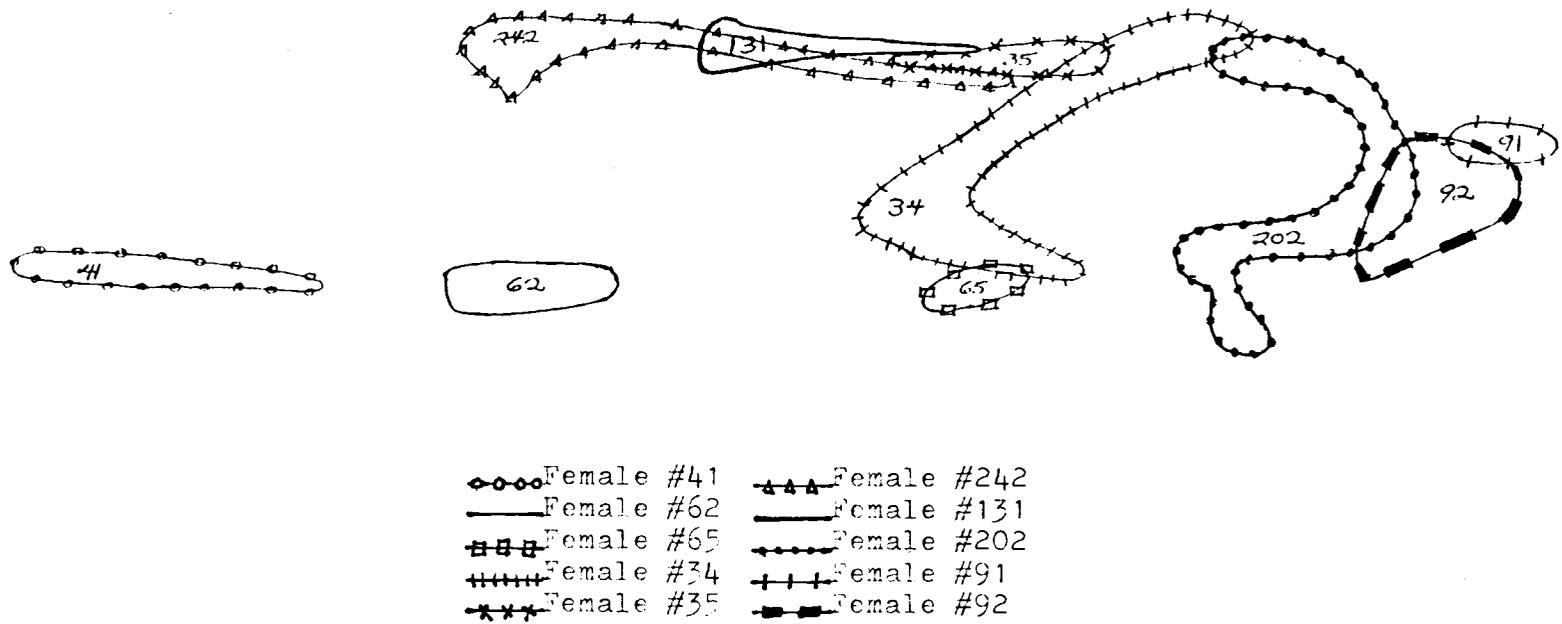


Figure 7b. Overlap of the home core areas of adult female *S. beecheyi* at Pigeon Butte in 1977. Numbers indicate an individual female.

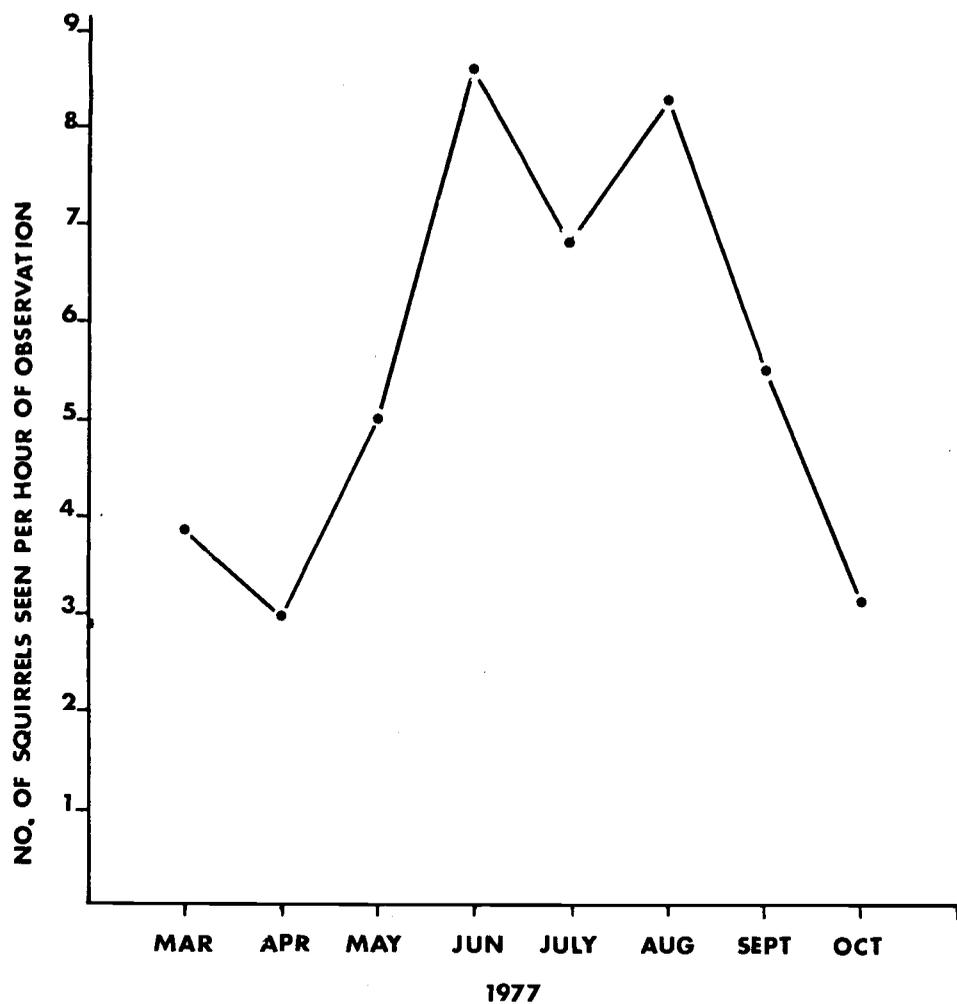


Figure 8. Number of *S. beecheyi* seen per hour of observation at Pigeon Butte from March through October, 1977.

Table 1. Hours of observation per day and daily frequency of encounter types for S. beecheyi at Pigeon Butte, Finley Wildlife Refuge, during March, 1978. Daily encounter rates for each type of encounter (aggression (AGG), displacement (DISP), male paw push (MPP), greeting/investigation (GI), approach/withdrawal (AW), and follow (FOLL)) are shown in parentheses and graphed in Figure 9.

<u>Day</u>	<u>Hrs. of observ. per day</u>	<u>AGG</u>	<u>DISP</u>	<u>MPP</u>	<u>GI</u>	<u>AW</u>	<u>FOLL</u>	<u>Enc. per day</u>	<u>(Enc. Rate)</u>
3/10	1.50	0 (.00)	0 (.00)	0 (.00)	2 (1.33)	0 (.00)	1 (.67)	3	(2.00)
3/12	4.50	12 (2.67)	0 (.00)	5 (1.11)	0 (.00)	1 (.22)	4 (.89)	22	(4.89)
3/16	2.50	1 (.40)	0 (.00)	6 (2.40)	2 (.80)	0 (.00)	2 (.80)	11	(4.40)
3/17	3.25	14 (4.31)	2 (.67)	4 (1.23)	0 (.00)	0 (.00)	6 (1.85)	26	(8.00)
3/18	3.00	14 (4.67)	0 (.00)	2 (.67)	0 (.00)	2 (.67)	1 (.33)	19	(6.33)
3/19	3.50	8 (2.29)	0 (.00)	2 (.57)	0 (.00)	1 (.29)	1 (.29)	12	(3.43)
3/20	2.00	6 (3.00)	0 (.00)	0 (.00)	0 (.00)	0 (.00)	0 (.00)	6	(3.00)
3/21	1.75	0 (.00)	0 (.00)	0 (.00)	0 (.00)	0 (.00)	1 (.57)	1	(.57)
3/31	1.75	0 (.00)	0 (.00)	0 (.00)	0 (.00)	0 (.00)	0 (.00)	0	(.00)
Total	23.75	55 (2.32)	2 (.08)	19 (.80)	4 (.17)	4 (.17)	16 (.67)	100	(4.21)

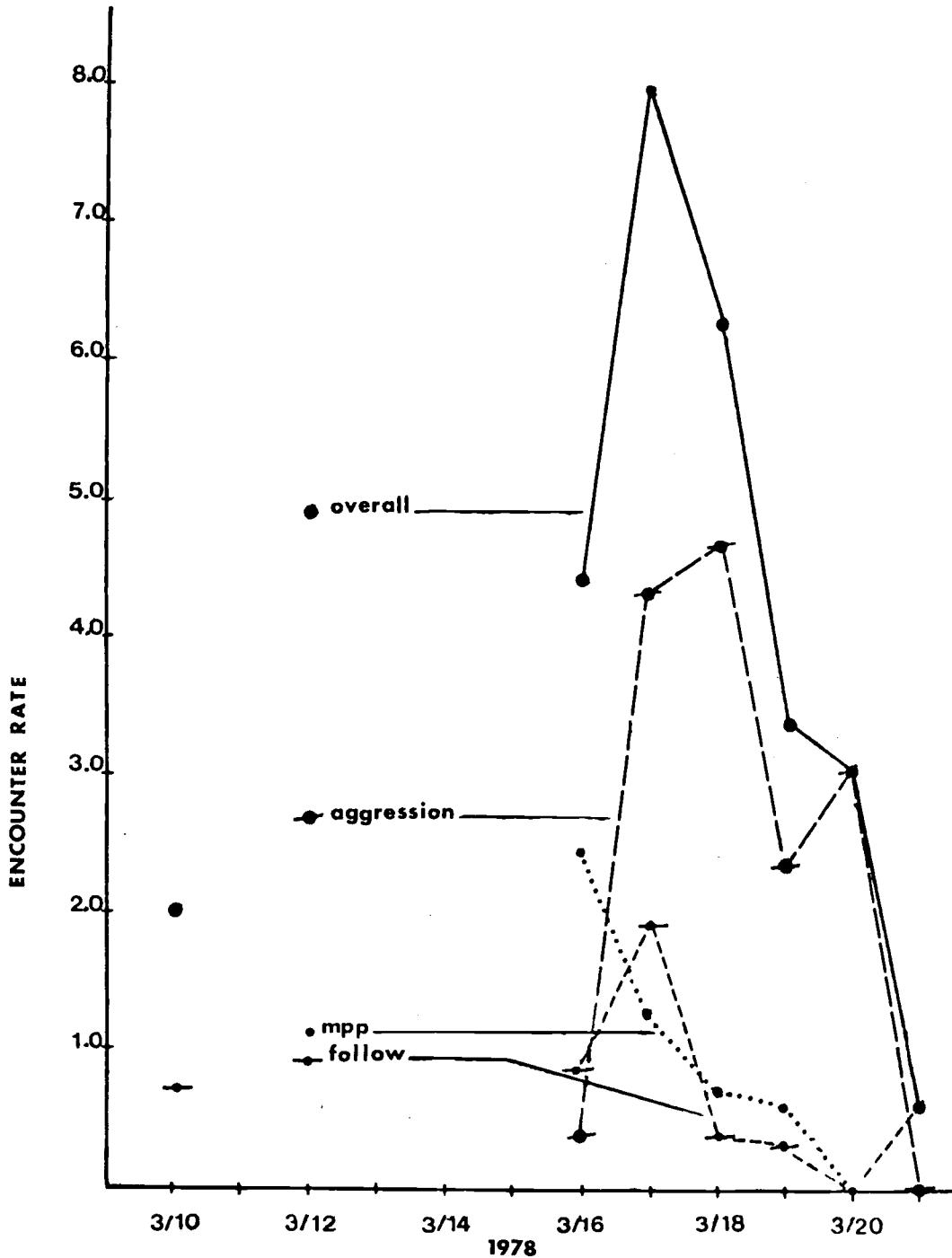
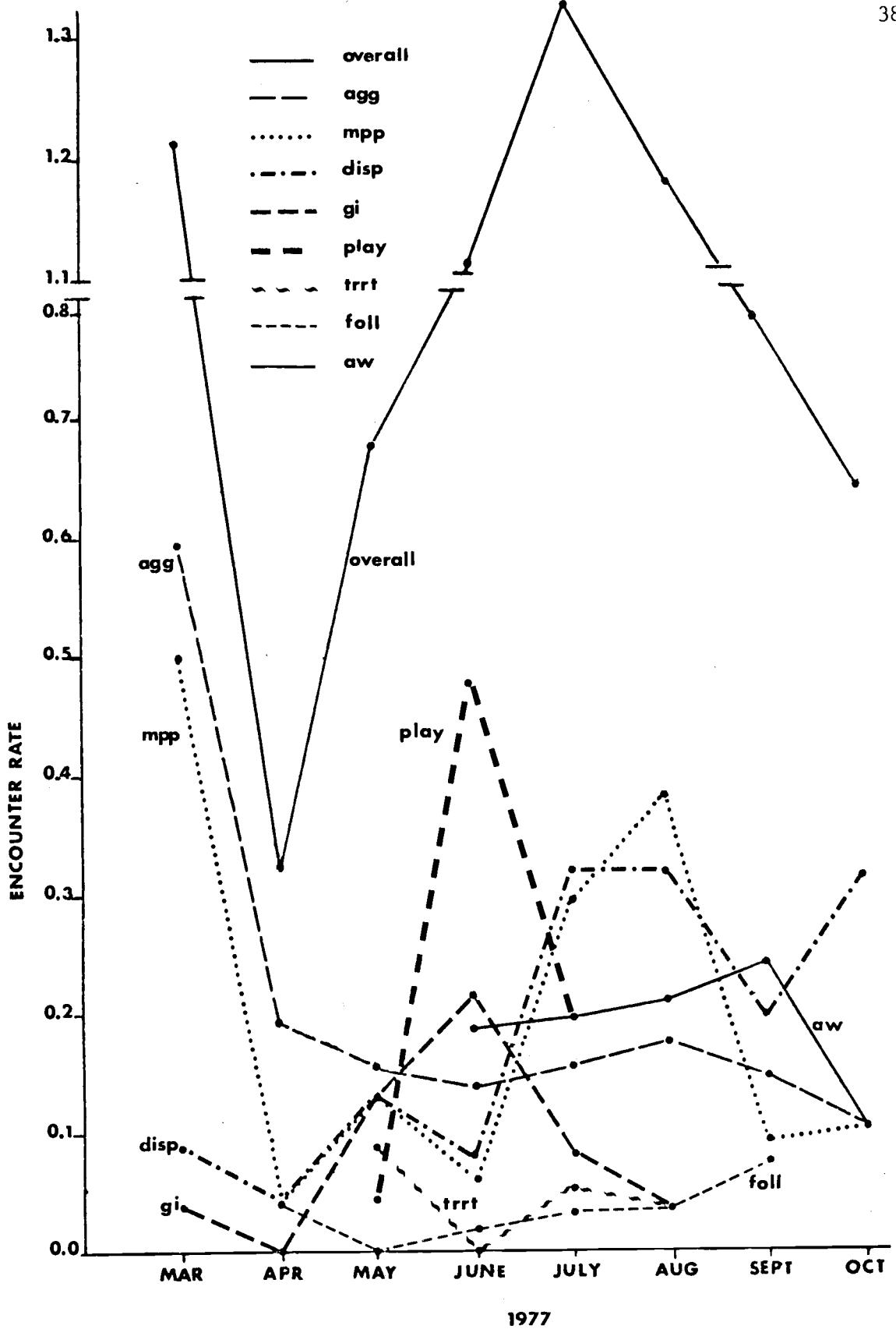


Figure 9. Daily encounter rates (number of encounters per hour of observation) of *S. beecheyi* at Pigeon Butte, Finley National Wildlife Refuge, during March, 1978. Solid line represents rate of all encounters (overall). Other lines indicate rates of aggression, male paw pushing (mpp), and following. Graphed from data in Table 1.

Table 2. Hours of observation per month and monthly frequency of encounter types for *S. beecheyi* at Pigeon Butte, Finley Wildlife Refuge, from March to October, 1977. Monthly encounter rates for each type of encounter (aggression (AGG), displacement (DISP), male paw push (MPP), play, greeting/investigation (GI), approach/withdrawal (AW), follow (FOLL), and turn-rear-raise-tail (TRRT)) are shown in parentheses and graphed in Figures 10-16.

Month	Hours of Observation per Month	AGG	DISP	MPP	PLAY	GI	AW	FOLL	TRRT	Enc.	
										Mo.	Rate
										<u>Total</u>	
March	22.25	13 (.58)	2 (.08)	11 (.49)	0 (.00)	1 (.04)	0 (.00)	0 (.00)	0 (.00)	27	(1.21)
April	47.00	9 (.19)	2 (.04)	2 (.04)	0 (.00)	0 (.00)	0 (.00)	2 (.04)	0 (.00)	15	(0.32)
May	45.75	7 (.15)	6 (.13)	6 (.13)	2 (.04)	6 (.13)	0 (.00)	0 (.00)	4 (.09)	31	(0.68)
June	50.75	7 (.14)	4 (.08)	3 (.06)	24 (.47)	11 (.22)	6 (.12)	1 (.02)	0 (.00)	56	(1.10)
July	57.75	9 (.16)	18 (.31)	17 (.29)	11 (.19)	5 (.09)	11 (.19)	2 (.03)	3 (.05)	76	(1.32)
August	29.00	5 (.17)	9 (.31)	11 (.38)	0 (.00)	1 (.03)	6 (.21)	1 (.03)	1 (.03)	34	(1.17)
September	21.00	3 (.14)	4 (.19)	2 (.10)	0 (.00)	0 (.00)	5 (.24)	2 (.10)	0 (.00)	16	(0.76)
October	29.00	3 (.10)	9 (.31)	3 (.10)	0 (.00)	0 (.00)	3 (.10)	0 (.00)	0 (.00)	18	(0.62)
Total	302.50	56 (.18)	54 (.18)	55 (.18)	37 (.12)	24 (.08)	31 (.10)	8 (.03)	8 (.03)	273	(0.90)

Figure 10. Monthly encounter rates (number of encounters per hour of observation) of S. beecheyi at Pigeon Butte, Finley NWR, during March through October, 1977. Solid line represents rate of all encounters (overall). Other lines indicate rates of aggression (agg), male paw pushing (mpp), displacement (disp), greeting/investigation (gi), play, turn-rear-raise-tail (trrt), following (foll), and approach/withdrawal (aw). Graphed from data in Table 2.



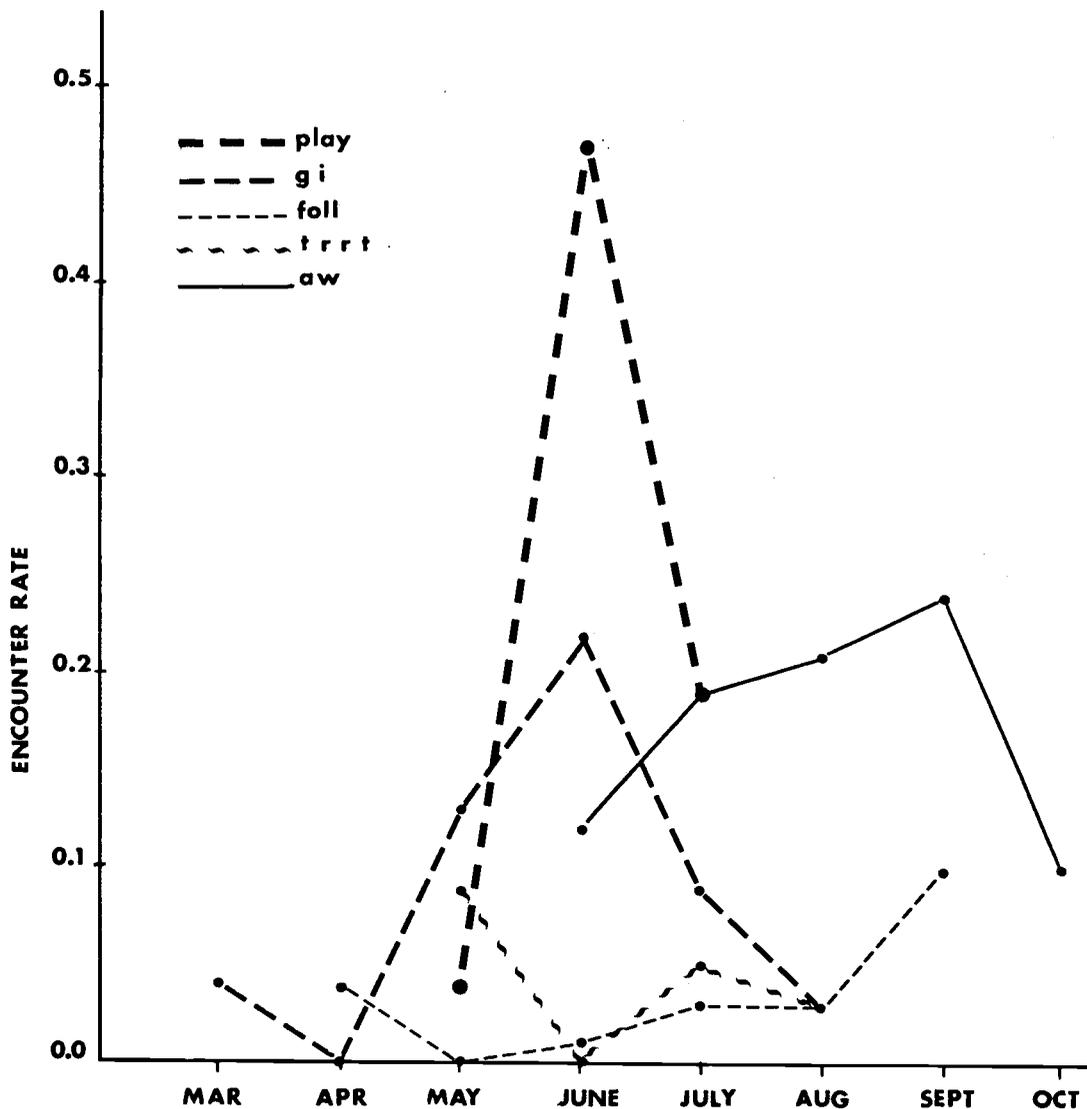


Figure 11. Monthly encounter rates (number of encounters per hour of observation) of encounter types frequently associated with juvenile *S. beecheyi*: play, greeting/investigation (gi), following (foll), turn-rear-raise-tail (trrt), and approach/withdrawal (aw). Encounters were observed from March - October, 1977 at Pigeon Butte. Graphed from data in Table 2.

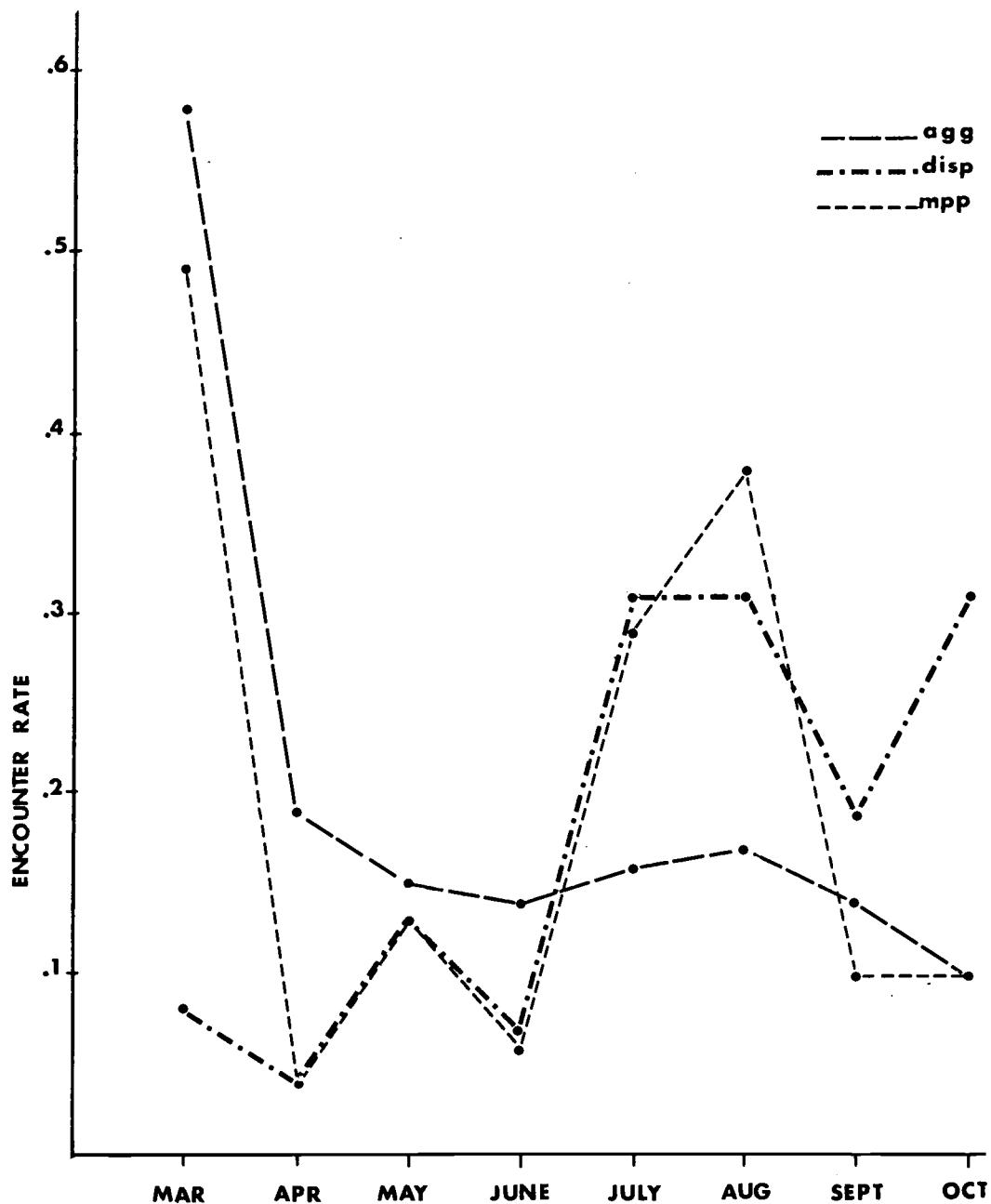


Figure 12. Monthly encounter rates (number of encounters per hour of observation) of encounter types frequently associated with adult *S. beecheyi*: aggression (agg), displacement (disp), and male paw pushing (mpp). Encounters were observed from March - October, 1977 at Pigeon Butte. Graphed from data in Table 2.

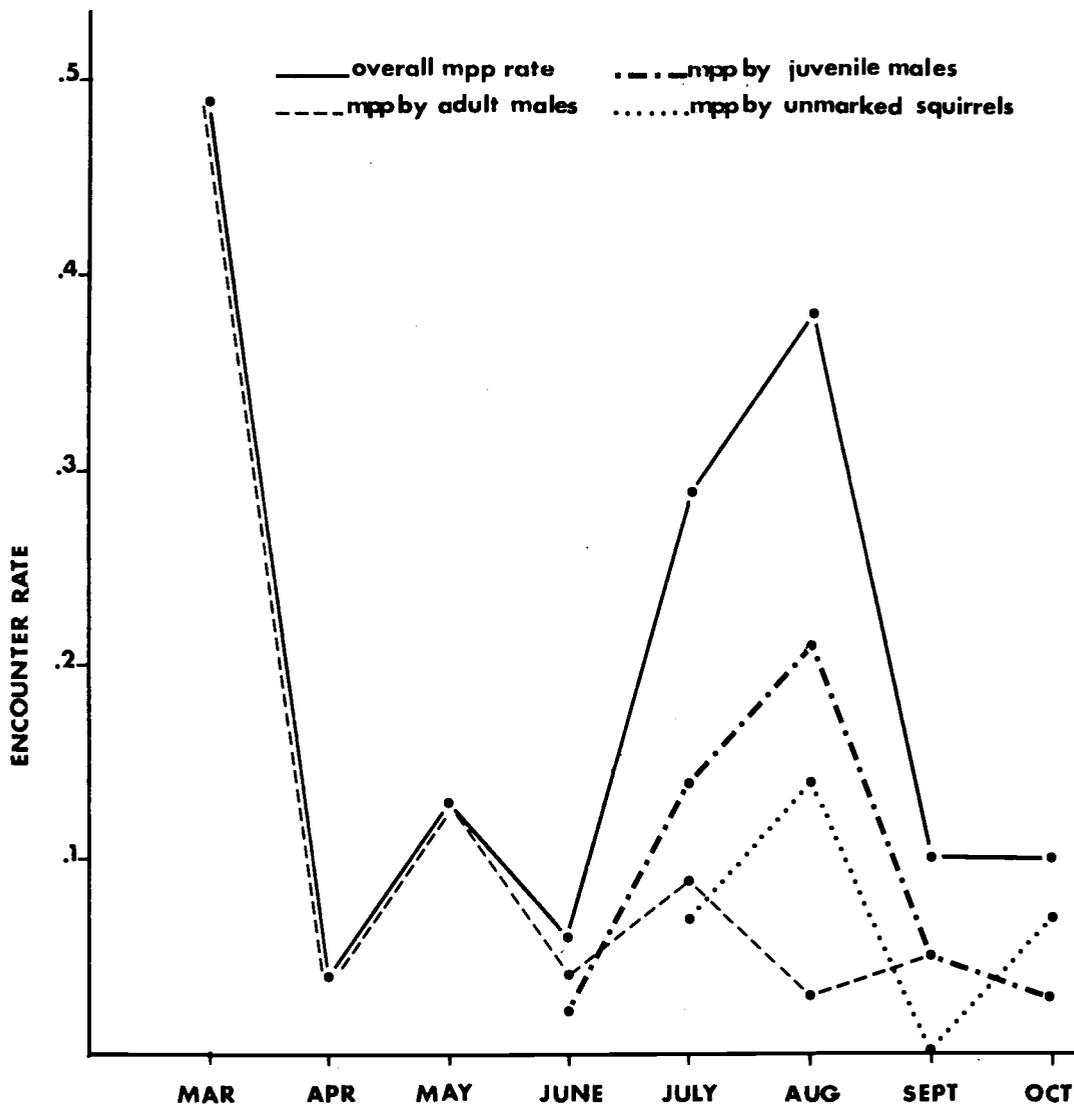


Figure 13. Monthly male paw pushing (mpp) encounter rates of *S. beecheyi* at Pigeon Butte from March - October, 1977. Solid line indicates overall mpp rate; other lines indicate rates with which was performed by adult males, juvenile males and unmarked squirrels.

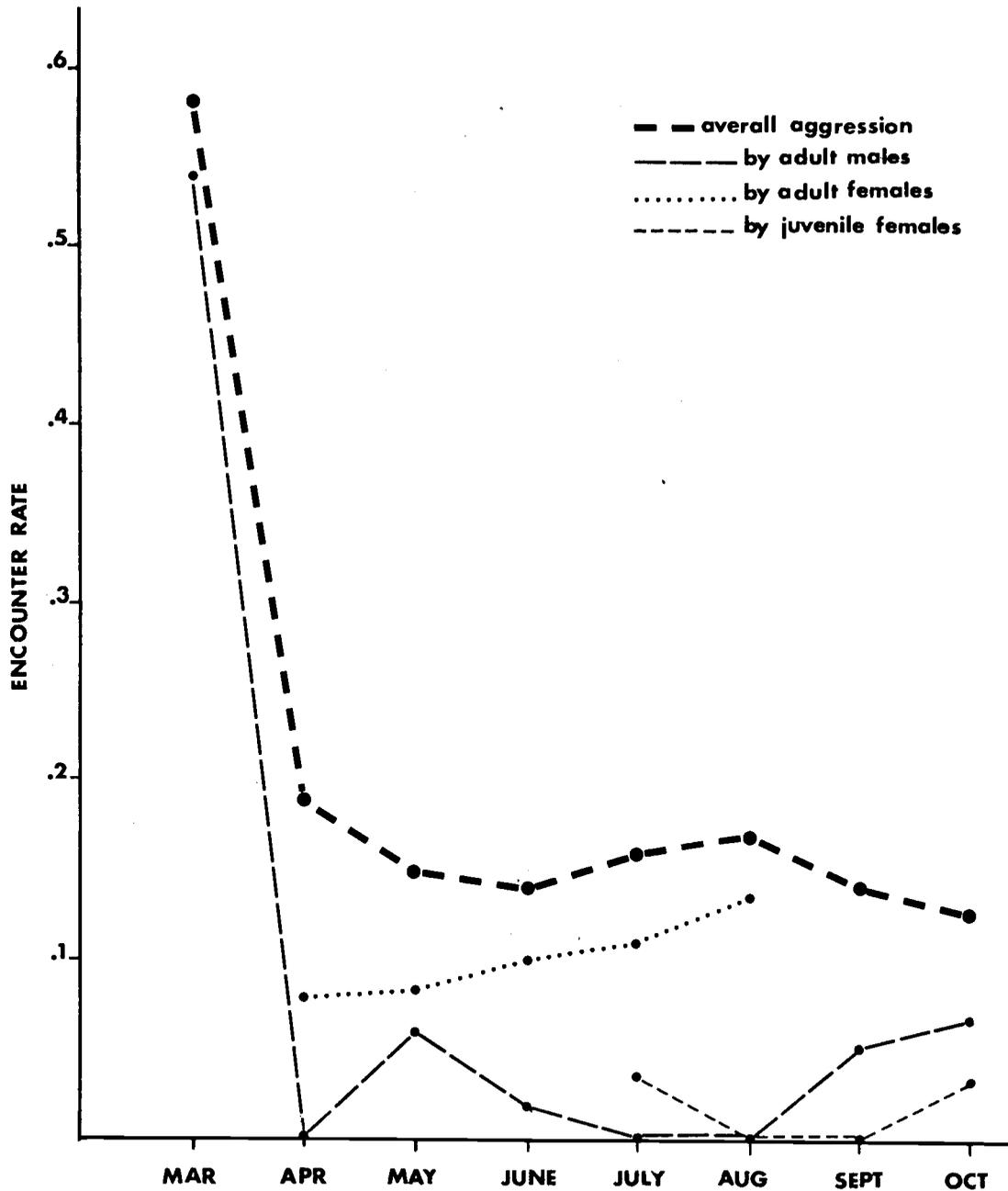


Figure 14. Monthly aggressive encounter rates of *S. beecheyi* at Pigeon Eutte from March - October, 1977. Top line indicates overall aggressive encounter rate; other lines indicate rates with which aggression was initiated by adult males, adult females and juvenile females.

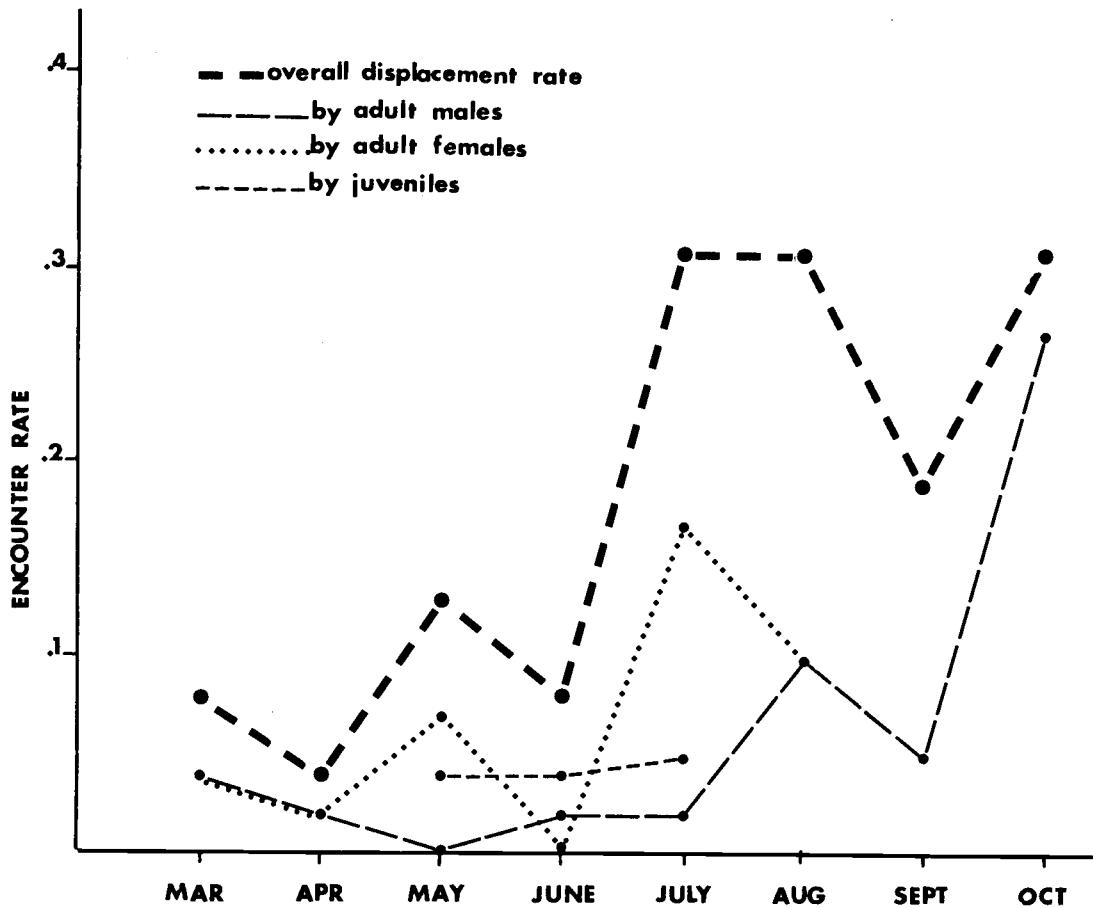


Figure 15. Monthly displacement encounter rates of *S. boeckeyi* at Pigeon Butte from March - October, 1977. Top line indicates overall displacement encounter rate; other lines indicate rates with which displacement was initiated by adult males, adult females, and juveniles.

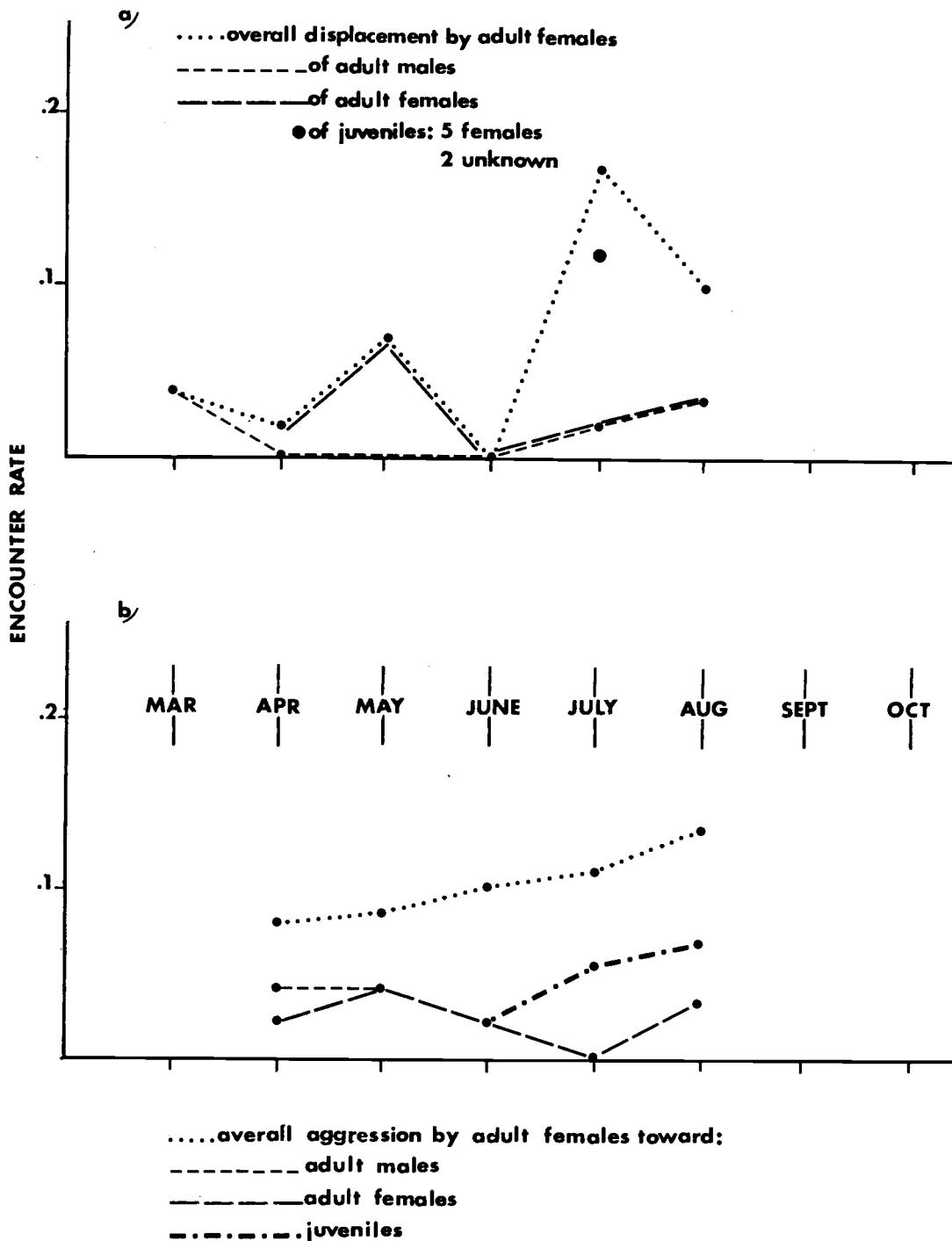


Figure 16. Monthly aggressive and displacement encounter rates of encounters initiated by adult female *S. beecheyi* at Pigeon Butte from March - October, 1977. a/ shows rates with which adult females displaced adult males, other adult females, and juveniles; b/ shows rates with which adult females chased adult males, other adult females, and juveniles.

DISCUSSION

Annual Cycle

The annual cycle of S. beecheyi can be divided into five phases: breeding (emergence from hibernation through copulation), pre-emergence of young (pregnancy to the emergence of young aboveground), litter (litter emergence to the dispersal of young from the burrow), pre-hibernation (litter break-up to hibernation), and hibernation (Dunford, 1977a).

Breeding Phase

In western Oregon, the breeding phase of S. beecheyi lasts from early February to late March. The males at Pigeon Butte emerged in early to mid-February and the females in late February to early March. The majority of sexual and aggressive encounters take place in mid-March, when the males establish breeding territories and court females.

Male aggression may prevent some males from establishing breeding territories. One yearling male won only one aggressive encounter out of 7 and he was never observed in courtship of a female. In contrast, another yearling male won 10 out of 12 aggressive encounters with 3 other males; 7 of these encounters were with one male. This yearling courted 2 females.

Most sciurids are polygynous and populations contain more adult females than males. My estimates for S. beecheyi ranged from 1.7 to 2.0 females per male; other investigators have estimated from 1.4 (Evans and Holdenried, 1943) to 2.3 females per male (Storer, 1944).

Although S. beecheyi males at Pigeon Butte courted several females, Linsdale (1946) reported a temporary pairing of male and female for as long as 2 weeks before the male moved to a new location. The actual period of sexual receptivity may be only a few hours. Sherman (1977) found that female S. beldingi were sexually receptive for a 4-6 hour period. Michener (personal communication, 1979) suggested that this was also true for S. richardsoni. Evidence implying synchronous breeding in S. beecheyi is that the majority of the mid-March, 1978 observations included more courtship and fighting than the early and late March, 1977 observations. In addition, most litters born in captivity during April, 1977, were born within a few days of each other (personal observation).

The spring territory established by a male overlapped the home ranges of several females. Owings, Borchert, and Ross (1977) observed that male home ranges had little overlap, while female home ranges overlapped extensively and were associated with the territory of a given male. The March, 1978 male home ranges at Pigeon Butte did not overlap as extensively as did the female home ranges, but female home ranges did not appear to be associated with any particular male territory. Each of the 5 marked males in the 1978 population had territories overlapping the home ranges of 3-6 females.

Pre-Emergence of Young

At Pigeon Butte, the pregnancy phase of S. beecheyi had begun by the end of March, and testes were ascending, as was typical for this time of year (Evans and Holdenried, 1943). The encounter rate dropped

to its lowest point of the season, and although males would occasionally approach and MPP females, no male aggressive behaviors were observed. Young were born 6-8 weeks prior to emergence aboveground in May (Evans and Holdenried, 1943). Prior to the emergence of the young, female aggression was directed toward males and other females in the form of chases and displacement.

Litter Phase

When the litter phase began in May, S. beecheyi littermates stayed close together and remained within about 10 meters of their burrow entrance. Female aggression increased toward both adult males and females. There were few instances of aggression among adult males and 7 MPP's directed toward adult females. In late May, juveniles participated in greeting/investigation and some play. Allogrooming was not observed in S. beecheyi. As the litter phase continued into June, juvenile play became the most frequent form of encounter. As juveniles wandered further from their home burrows and made contact with other squirrels, greeting/investigation encounters increased and approach/withdrawal encounters were observed.

Pre-Hibernation Phase

With the end of play in mid-July, greeting/investigation encounters declined in frequency. Adult female S. beecheyi became aggressive toward juveniles as the young dispersed throughout the quarry area. Females tended to chase juvenile males and displace juvenile females.

MPP encounters increased in both juveniles and adults. The recipients of MPP's were adult and juvenile males as well as adult and juvenile females. The response of the female recipients was often a

TRRT movement like that seen in spring courtship behavior. The frequency with which these encounters were seen increased in August. Approach/withdrawal movements directed toward a female and the following of females also increased.

The increased aggression by females in August preceded a decline of aggressive encounters prior to their entrance into hibernation in September and early October. The October increase in displacement and chases by adult males preceded their entrance into hibernation in early to mid-October. Evans and Holdenried (1943) and Fitch (1948) reported that the testes enlarged and descended in the fall, which would correlate with increased aggression. In S. undulatus, all members of one population fought in defense of burrows to be used for hibernation (Carl, 1971). While the increase in S. beecheyi aggression could be due to competition for hibernation sites, the squirrels were not defending a particular burrow area. Another explanation for increased aggression is that squirrels were harvesting acorns in late September and October. Squirrels from outlying areas of the quarry had to pass through the quarry to get to the oaks at the top of the hill; aggression by the residents of the quarry could have been directed toward these intruders. Most of the aggressive chases and displacement encounters in October were directed against unmarked squirrels by adult males.

Dispersal

At Pigeon Butte, 7 juvenile male S. beecheyi were last seen in July, possibly indicating dispersal from the colony triggered by adult female aggression. However, Yeaton (1972) reported that the midsummer

peak in S. richardsoni aggressive encounters was due to home range expansion by juveniles and their increased contact with adult females in adjacent territories. The fact that other S. beecheyi juveniles remained in the Pigeon Butte colony after July implies that no large-scale dispersal of young occurred at that time.

The retention of part of the mother's home range by female offspring may occur in S. beecheyi. Although my data was insufficient to show this trend, the one juvenile female still marked in 1978 had remained within her own and her mother's home range of 1977. Fitch (1948) reported that juvenile female S. beecheyi had a slight tendency to move from their original home ranges, while juvenile males dispersed by gradual stages.

Dunford (1977b) reported that male S. tereticaudus immigrated into the population in January and February, and that the population density increased to a peak at copulation followed by a decline in numbers of both sexes, especially males. Of the 14 S. beecheyi males marked in March, 1977, 4 of them were seen for only one day, 2 were not seen after the end of March, and 4 disappeared by the end of April. Of the 19 females marked that March, 4 were seen for only one day, 3 were not seen after the end of March, and 4 disappeared by the end of April. This disappearance of squirrels could be partly due to dispersal of yearlings or adults that were unmated or unable to establish breeding territories. Michener and Michener (1977) suggested that if dispersal occurred in the spring, immigration and emigration could be related to the number of squirrels that survived hibernation. A high overwinter survival rate and resulting high

population density could lead to dispersal.

Aspects of Social Structure and Sociality

While male and female S. beecheyi at Pigeon Butte lived independently of any group other than the mother/young unit, their home ranges overlapped extensively. Aggressive behavior occurred most frequently among breeding males, lactating females, and adult females encountering juveniles in July and August. Males sometimes performed approach/withdrawal or displacement grooming upon meeting neighboring males, but chased unfamiliar squirrels. Females often fed in the same area as other females, males and juveniles; however, females sometimes threatened if another squirrel approached too closely. The young greeted and played with each other, but no mutual grooming was observed. S. beecheyi tended to be tolerant of other individuals, but did not maintain a high level of cohesive behavior within the population.

The most social sciurids are those which exhibit a high frequency of cohesive behaviors, such as greeting and mutual grooming. Increasing sociality and cohesiveness correlates with delayed dispersal of young from the natal burrow, as in C. ludovicianus, M. olympus, M. flaviventris, and S. columbianus. The social structure of S. beecheyi was intermediate to the structures Kivett, et al. (1976) described for S. columbianus and S. franklinii. Adult male S. columbianus had a role in the defense of the group area and its residents, which included female adults, yearlings and young of the year. Yearlings dispersed but did not breed. In other spermophiles, mother and young formed the basic social unit for up to 2 months. The

mother/young bond lasted longest in S. undulatus, S. beecheyi and S. tereticaudus, and most briefly in S. tridecemlineatus and S. franklinii. Greeting behavior occurred in most spermophiles, but was infrequent in S. tridecemlineatus and S. franklinii (Wistrand, 1974; Kivett, et al., 1976).

Scent-marking behaviors of S. beecheyi were similar to those described for the more social spermophiles: twist marking, cheek rubbing, and dirt bathing. On the average, adult males performed more scent-marking behaviors than adult females. Some scent-marking areas were used repeatedly by several squirrels and received considerable olfactory attention from passing squirrels.

An important consideration in determining the social structure and sociality of a species is that most populations are observed for only one season. The degree of sociality of a species and its corresponding rates of social encounters vary with population density, the age and sex structure of the population, whether the population members have lived together previously, how space is shared among them, and the individual behavioral characteristics of the residents and potential recruits to the population (Armitage, 1977). For example, cohesive behaviors may be high in a population where the residents have lived together previously, but agonistic behaviors may be high if there are many immigrants present. Another consideration is that a species may exhibit a range of social structures and social behaviors at varying population densities. To accurately determine the effect of these factors on social structure, a species should be studied over a period of several years in different habitats and at different

population sizes. However, a year-long study can provide information as to the types of relationships and seasonal activity of a particular species.

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