

BEHAVIOR AND COMMUNICATION IN THE SHORT BARE-TAILED OPOSSUM

(Monodelphis domestica)

by

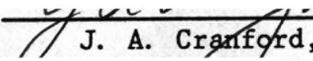
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(ABSTRACT)

Behavior and communication modes were studied in captive Monodelphis domestica, a small solitary, nocturnal, omnivorous marsupial in the family Didelphidae. The social biology was examined to evaluate the importance of visual, olfactory, auditory, and tactile communication. Social contexts were compared in 124 encounters of 30 min each. An ethogram was developed containing 74 behaviors which sorted into 9 major behavioral categories: grooming and resting, exploration, attention, scent marking, vocalizations, social contact, aggression, retreat, and sexual.

Solitary Monodelphis explored, groomed, and scent marked. Familiar male-female pairs displayed less aggression than unfamiliar male-female pairs. Non-estrous females aggressively repelled males and exhibited much dominance related behavior, but male-male pairs were the most agonistic. Seven scent marking modes were identified which functioned to communicate individual identity and sexual advertisement. Males could distinguish sex and estrous condition of conspecific urine donors by olfaction. Dig perineal dragging, lateral side rubbing, and hip rubbing were unique to Monodelphis. Tongue protrusion was observed and may be related to vomeronasal organ function. Four principal agonistic

vocalizations were used while one, clicking, was observed only in male sexual behavior and submissive contexts by both sexes. A chittering vocalization is described. Social contact behaviors included approaches and directed sniffs. Males sniffed female cloacal regions who in turn sniffed the males' sides and abdomens. Dominance-subordinance relationships were characterized.

Behavior of close relatives Didelphis and Marmosa was similar, but some behaviors were unique to Monodelphis.

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INTRODUCTION

The short bare-tailed opossum (Monodelphis domestica) is a small omnivorous-insectivorous marsupial in the family Didelphidae which inhabits the Brazilian caatinga (an arid scrubland) and has been described as socially solitary but nonterritorial (Mares et al. , 1981). Few studies have been done on this species' ecology, and its general and social behavior is for the most part unknown. Intraspecific communication is a major behavioral component by which individual animals communicate with one another through visual, chemical, auditory, and tactile modes (Smith, 1977). The importance of each of these communication modes depends on a number of factors including the animal's size, habitat, social organization, ecology, and activity patterns (Eisenberg, 1981). Factors of importance in determining behavior and communication modes in Monodelphis are its morphology and ecology.

This study utilized staged behavioral encounters (Eisenberg, 1966) to characterize a laboratory ethogram (behavioral catalogue) for Monodelphis and to characterize the function of specific behaviors used in various social contexts. Behavior categories used were: grooming and resting, exploration, attention, scent marking, vocalizations, social contact, aggression, retreat, and sexual. Auditory and olfactory communication modes were studied due to their apparent importance to solitary nocturnal species (Eisenberg and Golani, 1977). Olfactory preference associations were evaluated using urine stimuli to determine the relative importance of these chemical communication signals in Monodelphis.

Vocalizations of Monodelphis were recorded within their social context in order to characterize their probable function. Comparisons were made to other didelphid species in order to evaluate behavioral differences which may be related to differences described in the species' ecology.

REVIEW OF LITERATURE

The short bare-tailed opossum (Monodelphis domestica) (Wagner, 1842) is a small marsupial in the family Didelphidae found in eastern and central Brazil (Collins, 1973); Bolivia (Pine, 1979); and Paraguay (Myers and Wetzel, 1979). The genus Monodelphis is the smallest in the family Didelphidae (Hershkovitz, 1969). Twelve species are currently recognized in the genus Monodelphis, however, Pine (1979) speculates that M. domestica may actually be more than one species because of the wide variation in the skulls he has examined.

Total body length of Monodelphis domestica ranges from 160-205 mm while tail length ranges from 45 to 64 mm. Adult male weights range from 90 to 155 g and females from 80 to 100 g (Fadem et al., 1982). Monodelphis possess up to 27 teats and both sexes lack a marsupium (Hunsaker, 1977). Litter size varies from 3 to 14 young (Fadem et al., 1982).

The genus Monodelphis is primarily terrestrial, occurring near water in the forest undergrowth, and is often found near human habitation. Food resources include small rodents, insects, fruits, seeds, and carrion. Monodelphis has been reported by Kirsch (in Collins, 1973) from a mixed habitat of both grasses and short dicots less than thirty cm high. Myers and Wetzel (1979) found M. domestica in grassy areas, brush piles, and among rocks in a dry river bed. Collins (1973) reported that they build nests on the ground in fallen hollow logs or rock piles. Mares et al. (1981) found M. domestica to be a common mammal in the Brazilian caatinga preferring rocky areas. The caatinga is a xerophytic thorn scrub

habitat in the northeastern interior of Brazil (Tricart, 1972; Mares et al., 1981). The rainy season lasts from November to March with 500-1100 mm of rain falling, with 25-150 mm of rainfall occurring in the dry season (July - September) (Tricart, 1972). Average annual temperature range is from 22° to 27°C.

The ecology of six species of didelphids was studied by O'Connell (1979) (Didelphis marsupialis, Marmosa fuscata, Marmosa robinsoni, Philander opossum, Caluromys philander, and Monodelphis brevicauda) in northern Venezuela for two years by mark and recapture methods. Most species were found to be seasonally polyestrous with timing of rainfall being an important factor determining reproductive patterns. Monodelphis brevicauda breed between May and September, producing two litters which results in weaning of young during the rainy season when food is abundant. Didelphis, Caluromys, and Marmosa all appear to follow this same pattern of breeding and producing young as food availability increases (O'Connell, 1979). Most of the South American marsupials appear to be seasonal breeders (Tyndale-Biscoe and MacKenzie, 1976; Flemming, 1973; O'Connell, 1979). Monodelphis domestica was found to be a year-round polyestrous breeder (Streilein, 1982c), in the Brazilian caatinga where seasonal rainfall was unpredictable (Streilein, 1982f); however, most of this field work was carried out during 2 years of above normal precipitation (Mares et al., 1981). Granitic outcrops serve as mesic microrefugia, permitting year-round breeding (Streilein, 1982b,d). Monodelphis domestica has been reported to be a good water conserver (Christian, 1983), which would better adapt it to this arid habitat.

Monodelphis domestica is a nomadic animal with residency time on a 2.7 ha grid always less than one year. Two litters were the maximum known for a single female, because of low residency time on the grid. A female could potentially produce 5-6 litters per year under optimal conditions (Streilein, 1982c). Sexual maturity is reached in approximately 3-7 months (Trupin and Fadem, 1982) and females weighed at least 50 g to reproduce (Streilein, 1982c). Monodelphis population density in the caatinga increased during the dry months as a result of maturation of subadults produced during the wet season. Home range size was estimated at 1472 m², with male ranges averaging somewhat smaller than that of females (Streilein, 1982c).

The estrous cycle of this species is approximately 28 d with behavioral estrus lasting 36 h. Gestation lasts 14 to 15 d with the young born one cm long and weighing about 100 mg (Fadem et al., 1982). Since gestation falls entirely within the estrous cycle in marsupials, successful parturition and lactational feedback by nursing young inhibits the next estrus. If a litter is lost the female returns to estrus, mates, and attempts to rear another litter (Sharman, 1970). Young Monodelphis detach from the teats about two weeks post partum weighing 2-3 g (Fadem et al., 1982), which is very comparable to the mass of an equivalent sized altricial eutherian at birth (Sharman, 1970). Young hang on to the female's body, moving to her back as they grow older, and are weaned at about 7 weeks of age (Fadem et al., 1982).

Didelphid Behavior

Communication in marsupials was reviewed by Eisenberg and Golani (1977) who reported that olfactory and auditory modes of communication are probably more important for nocturnal marsupials than the visual mode.

McManus (1970) studied the behavior of captive Didelphis virginiana including locomotory, exploratory, defense, escape, feeding, defecation, grooming, resting, sleeping, nest building, vocalizations, scent marking, and social behavior. Encounters between two adult males, two adult females, and adult males and females were observed in outdoor enclosures for periods ranging from several hours to two weeks. Social behavior between two adult males was typically agonistic with sexual recognition apparently determined by olfaction. Clicking sounds were emitted in addition to growls and screeches. Females were observed to be aggressive toward each other with fights occurring, but were less violent than males in dyad encounters. No clicking occurred as in male-male encounters. Unlike the males, females became tolerant of each other with time. In male-female pairings, males showed immediate sexual interest, while the responses of the female depended upon her estrous cycle. Males nuzzled females in the genital region, emitted clicking vocalizations and attempted to mount. Females not in estrus responded aggressively. Aggression by females toward males was not as severe as that between males. Males were not observed to bite back and responses were either sexual or submissive. Submissive response of the male involved lowering and turning the head to the side, and facing away from the female. After several days

together, males usually ignored the females. McManus (1970) concluded that social behavior is poorly developed in Didelphis.

Didelphids were studied in Guyana by Charles-Dominique (1983) who found few interspecific differences in anatomy or social structure between species. The small differences found could be correlated with ecological differences, particularly between the more omnivorous, terrestrial Philander opossum and the more frugivorous, arboreal Caluromys philander.

Didelphis virginiana and most of the other didelphids are solitary except when breeding or when a female has young. Agonistic behavior is the most common form of behavior in Didelphis (Hunsaker and Shupe, 1977). Some aspects of Monodelphis domestica behavior have been described by Hayssen (1980) who reported it to be very reclusive — spending up to 56% of the night in nest boxes, while females with young spend up to 83% of the night in nest boxes. Streilein (1982a) found M. domestica in the caatinga most active for a few hours after dusk. Captures were primarily on the ground, but the animals were adept at climbing. Nest building behavior was described by Unger (1982) who suggested that the tri-layered nests possibly function to protect the animal from diurnal heat. Nesting material is carried with the tail as in Didelphis (Hayssen, 1980; Unger 1982). General behaviors briefly described by Streilein (1982e,f) include: exploration, grooming, prey capture, and agonistic behavior. Threats, lunges, and fights occurred in most encounters. Sexual behavior between male and female Monodelphis domestica begins when males are placed with a female (Trupin and Fadem, 1982). Non-receptive females were

very aggressive toward males, but receptive females eventually permitted copulation.

The general pattern of social organization in didelphids was described by Charles-Dominique (1983). Members of this family are nomadic and do not maintain territories in the sense of an exclusive defended area. Overlapping of home ranges occurs with only individual distance being defended against conspecifics, and home ranges tended to drift in location with time. During the breeding season, males move around more than females. Social bonds between individuals do not persist after weaning, and all subsequent encounters between adults are either for reproduction or are agonistic.

Olfactory Communication

Olfactory modes of communication in mammals have been well documented (Ralls, 1971; Eisenberg and Kleiman, 1972; Johnson, 1973). Special body movements have evolved in many mammals for distributing chemical substances and has been termed "scent marking" (Ewer, 1968). This includes odor dispersal by urination, defecation, salivation, secretion of glandular material, and vaginal secretions (Kleiman, 1966; Ralls, 1971; Epple, 1974a,b). The term "pheromone" is generally used to describe any kind of chemical communication among conspecifics (Epple, 1974a). There are two basic pheromonal types — primers and releasers. Releasers cause an immediate behavioral reaction in the receiver, while primers cause slow physiological responses (Whitten, 1975). Species specificity, well defined behavioral or endocrinological function, and genetic programming

with a minimal amount of learning experience are three characteristics commonly associated with mammalian pheromones. Additionally, the message a particular chemical sends may vary depending on the receiver and the context in which it is received (Beauchamp et al., 1976).

Commonly proposed functions of scent marks are: identity of the individual, its sex and reproductive condition, and its species or subspecies. Other activities associated with scent marking are courtship, pairbonding, coordination of mating activity, synchronizing reproduction, and as a substitute or deterrent for aggression (Eisenberg and Kleiman, 1972; Epple, 1974a,b, 1976; Johnson, 1973; Ralls, 1971; Smith, 1977). Functions of chemical signals are commonly determined by presenting urine, feces, glandular exudate, or scent marked objects to conspecifics in an arena, olfactometer, or home cage. By varying donor animals and presenting the subject with two chemical choices, preferences for one of the chemical signals can be determined by preference paradigm (Doty, 1975). The dependent variable measured is generally the amount of time spent sniffing each chemical. A discrimination between the two is assumed if one sample is investigated more than the other (Dunbar, 1978). Experimental design must counter-balance the presentation schedule to avoid subject habituation (Doty, 1975). In callithricids this method has determined that animals could distinguish scent marked perches by individual, species, and sex of donor (Epple, 1973; 1974a,b). Gerbils and guinea pigs also distinguish their species from others by ventral glandular sebum and urine (Thiessen et al., 1970; Beauchamp, 1973). Sex of the donor individual can be distinguished by glandular sebum in gerbils (Thiessen et al., 1970), and in dogs and guinea pigs presented with urine (Dunbar,

1978; Beauchamp, 1973). Squirrel monkeys and guinea pigs distinguish individual conspecifics by scent (Kaplan and Russell, 1974; Berüter et al., 1974). Reproductive status of females can be determined by conspecific males via vaginal secretions in rhesus macaques (Michael, 1969; Michael et al., 1975) and by urine in dogs (Dunbar, 1978) and rats (Pfaff and Pfaffmann, 1969).

Relatively little is known about communicative function of chemical secretions and olfactory communication in marsupials. Schultz-Westrum (1970) has studied sugar gliders (Petaurus breviceps) in social groups where the males mark all members with that group's odor. Among the New World marsupials, Didelphis possess sternal glands, anal sacs, foot pad glands, and proctodeal glands (Müller-Schwarze, 1983). The behavior of Didelphis includes two types of scent marking — a perineal rub and saliva rubbing (McManus, 1970). Perineal rubbing in both sexes was frequently followed by defecation and saliva rubbing (Reynolds, 1952). A territorial or agonistic function was associated with these since males sometimes responded to it with an aggressive display. Didelphis has also been reported to mark with the cheek region (Hunsaker and Shupe, 1977). McManus (1970) found Didelphis paid no attention to conspecific urine, yet urine marking has been found to be an important olfactory communicatory channel in other marsupials (Eisenberg and Golani, 1977).

Feces, or glandular deposits on the feces, appear to be of some importance to olfactory communication in some marsupials (Eisenberg, 1981). The major body areas rubbed or marked by marsupials are the cloaca, cheek or chin region, and the sternum (Eisenberg and Golani, 1977).

In the murine opossum (Marmosa robinsoni) dominant males used sternal glands to mark the enclosure, but exhibited no obvious reactions when they encountered previously marked areas (Hunsaker and Shupe, 1977). Some species of Marmosa have well developed glands while in others they are undetectable. Other didelphid genera probably also have active sternal glands used particularly for marking during the reproductive season. Monodelphis has well developed sternal glands which produce a strong odor (Hunsaker and Shupe, 1977).

A complex scent marking system is found in Monodelphis domestica (Streilein, 1982f). Areas of the body reportedly used for scent marking include: the cheek, chin, flank, sternum, and perineal region. Messages transmitted by scent marks have not been extensively investigated in didelphids as they have in some eutherians (Eisenberg and Golani, 1977).

Auditory Communication

Auditory communication is an important mode particularly for nocturnal mammals (Eisenberg and Golani, 1977). Responses to vocalizations depend on the contexts in which the sounds are emitted. In some small nocturnal mammals the vocalizers' location and level of arousal are the principal messages (Gould, 1969; Eisenberg and Gould, 1970; Gould, 1983). Often vocal signals are part of a stimulus which also involves a visual display. Most marsupial vocalizations fall into this category since they are usually of low intensity and occur during social encounters (Eisenberg et al., 1975).

Marsupial vocalizations are classified into four syllable types (Eisenberg et al., 1975). Type I sounds are tonal, non-aggressive, and are produced in mother-young, submissive, or courtship contexts, and include chirping sounds in young Marmosa and Caluromys. Type II sounds (growls and screeches) are composed of overlapping tonal mixtures. Type III sounds (clicking) are less than 0.02 s in duration and are usually repeated. Lastly, Type IV sounds are non-harmonic vocalizations such as a hiss. Among the didelphids, only Caluromys, the woolly opossum, has been reported to have a loud, aggressive distress call audible up to 200 m away (Charles-Dominique, 1983). Generally harsh low frequency sounds are associated with agonistic situations while higher frequency tone-like sounds are more characteristic of non-aggressive, fearful, or appeasement situations (Morton, 1977). This is true for the didelphids where three out of the four basic vocalizations are emitted during agonistic situations (hisses, growls, and screeches) (Hunsaker and Shupe, 1977), while clicking is given in several contexts (sexual behavior in males, mother-young contexts, and submissive situations) (McManus, 1970; Hunsaker and Shupe, 1977; Eisenberg and Golani, 1977).

Clicks are short low intensity atonal sounds (Eisenberg et al., 1975) which are produced in Didelphis virginiana by smacking the lips (McManus, 1970) at regular 0.4 s intervals (Hunsaker and Shupe, 1977). Marmosa robinsoni produces clicks lasting 0.0146 to 0.0155 s at intervals of 0.0042 s (Eisenberg et al., 1975). Clicks are also emitted by young Philander opossum and Caluromys philander (Charles-Dominique, 1983), while an analogous clicking sound is produced by the teeth in Trichosurus vulpecula, the brush possum of Australia (Wemmer and Collins, 1978).

Clicks are easily produced and localized, and may be the most universal of mammalian sounds (Gould, 1983).

A hissing vocalization is common in didelphids, and is a low amplitude sound in Didelphis with a duration of 1-2 s (Hunsaker and Shupe, 1977). Several subtypes of hissing were found in Marmosa of durations between 0.0025 and 0.03 s with most of the energy concentrated between 1 and 2 kHz (Eisenberg et al., 1975). Hissing is a low level agonistic threat that is associated with defensive postures (Hunsaker and Shupe, 1977) and probably results from air expulsion as the thoracic region tenses. Should the stimulus eliciting the hiss in Didelphis persist, vocalization intensity increases into a growl (McManus, 1970).

Growls are the most common vocalization in Didelphis, having a duration of 1.5 s and frequencies ranging between 0.5 and 8 kHz (McManus, 1970). Growling amplitude increases as young opossums become adults (Hunsaker and Shupe, 1977). Hissing and growling are close contact calls likely to function to intimidate the receiver (Eisenberg et al., 1975). If the stimulus inducing the growl intensifies, the vocalization produced develops into a screech (McManus, 1970).

Screeches are characteristic of the highest levels of aggression in didelphids. A screech in Didelphis is typically 0.7 s in duration and has energy filling the range 1 to 16 kHz or higher (McManus, 1970). Screeching may serve as a general alarm reaction and also alert other animals of an encounter (Hunsaker and Shupe, 1977).

Monodelphis domestica produce the clicking and hissing vocalization (Hayssen, 1980) as do other didelphids as well as growls and screeches (Streilein, 1982f). Growls were rarely heard in intraspecific encounters

between Monodelphis and the screech was not noted (Trupin and Fadem, 1982); however, a spitting vocalization was reported in highly aggressive contexts. Clicking has been reported only in male Monodelphis (Hayssen, 1980; Trupin and Fadem, 1982), with a frequency of 6-7 / s. Young Monodelphis produce ultrasonic vocalizations before releasing from the teats (Gould, pers. comm.) and the species is responsive to sounds above 20 kHz (Hayssen, 1980).

MATERIALS AND METHODS

Six pairs of Monodelphis domestica were obtained from the National Zoological Park (Smithsonian Institution, Washington, D.C.). The subjects were descended from 4 males and 5 females captured in May, 1978 in the caatinga region near Exu in the State of Pernambuco, Brazil. Animals were set up as bisexual pairs in cages (home cages) measuring 60 x 60 x 60 cm or 37 x 42 x 28 cm with one nest box for each animal. Small pine bark chips were used as a substrate. Animals were fed a mixture of meats, marmoset diet, canned dog food, laboratory rat or mouse pups, crickets, bananas, apples, and milk, with water available ad lib. Pervinal was dusted periodically on the food as a vitamin supplement. Cages were maintained in a small underground cinderblock building located on the Virginia Polytechnic Institute and State University (V.P.I. & S.U.) campus on an LD 12:12 photoperiod and maintained between 21-23°C. These six pairs produced an additional 10 offspring which were used in the neutral test encounters. Young animals were housed under adult conditions after weaning. Twenty-two individuals (11 males and 11 females) were available for the six experimental contexts.

To compile a basic catalogue (ethogram) of the behaviors exhibited by Monodelphis, twelve animals were observed within all experimental contexts for varying periods of time totaling 25 h. Animals were observed in the home cages and in arenas (1 x 1 x 1 m) between January and June, 1981. The content of the behavioral ethogram was used as the basis for quantification of the observed behaviors in neutral test encounters.

Neutral test encounters of single and paired adults were carried out in a 1 x 1 x 1 m clear plexiglas arena with only substrate present. Observations were carried out under red light illumination from June 1981 through November 1982 and began 30 min after dark onset. Pine bark was used as a substrate, and between successive encounters it was changed and the arena cleaned with methanol to remove any prior olfactory traces (Epple, 1978). In paired animal experiments the animals were initially separated by a clear plexiglas divider for 5 min before interactive behavior was permitted. When two animals could not be easily recognized, a small piece of tape was placed on the back of an individual chosen randomly. Behaviors of two interacting animals were recorded for 30 min by hand on data sheets. Each behavior was designated by a one or two letter abbreviation for more rapid recording. Behaviors were totaled by category occurring during the encounter. These were grouped into ten major behavioral categories: grooming and resting, exploratory, attentive, scent marking, vocalizations, social contact, aggressive, retreat, and sexual. An "other" category included behaviors not naturally falling into a particular context (e.g. jumping at the sides of the arena). One hundred twenty-four encounters utilizing 22 opossums were observed between June 1981 and November 1982 with interaction schedules planned such that no individual was used proportionately more or less often than any other. Mean intervals \pm S.D. between individual reuse were 24 ± 3.8 days for males and 31 ± 5.2 days for females. Within an encounter context, no individual animal pair combination was run more than once. Encounter contexts observed and sample sizes were: solitary males (14), solitary females (14), familiar male-female pairs (co-caged for at least two

weeks)(15), unfamiliar male-female pairs (both individuals were unfamiliar)(40), dyad males (two males unfamiliar with each other)(21), and dyad females (two females unfamiliar with each other)(20).

To further examine olfactory, auditory, and tactile communication modes, data from the neutral test encounters were subdivided into their discrete behavioral components to determine how modes of scent marking, vocalization types, and social contact behaviors vary between encounter contexts.

Dominance-subordination relationships were determined for the male dyads and female dyads by classifying dominant individuals as those approaching, chasing, or restricting the movement of the other pair member who retreated or otherwise exhibited avoidance behavior, and was therefore classified as the subdominant individual. Comparisons between behavior of dominant and subdominant individuals were carried out for the major behavioral categories from the neutral test encounters and also for the behavioral components of scent marking, vocalization, and social contact.

Data are presented in the form of box plots (Koopmans, 1981) for each major behavioral category. Box plots were used in order to provide visual information about the data content. Scent marking, vocalization, social contact, and dominance-subordination comparisons are presented in box plots when significant differences occurred. Boxplots depict the data with the central 50% of the observations falling inside the box, 25% on each side of the median line with triangles marked to indicate means. Vertical lines extending from the box contain all values except outlying values. Open circles denote mild outliers and closed circles extreme

outliers. For plots with many zero values, the box lies on the horizontal axis. By observing the box plots, differences in distribution of behavior frequency can be seen between the different encounter types.

Overall median tests (Dixon and Massey, 1969) were performed on males and females for each behavioral category. If the overall intra-sex comparison was significant, individual median test comparisons were performed within a sex, between solitary males and solitary females, and between male and female dyads. Solitary animals are excluded from many of the major behavioral comparisons since more than one animal was necessary for some behaviors to be elicited. The median test is a non-parametric procedure testing the null hypothesis that two independent samples are from the same population with equal medians. In paired comparisons between familiar males and females, unfamiliar males and unfamiliar females, and dominant and subordinate individuals of the same sex, sign tests (Dixon and Massey, 1969) were used to test for significant differences. Sign tests are paired comparison procedures testing a null hypothesis that the paired animals in each comparison do not differ behaviorally.

Male Monodelphis were presented two sources of olfactory stimuli to determine if they exhibited an ability to discriminate between the two. Discrimination was determined by differential amounts of time spent in association with one of the stimuli. This was subsequently referred to as a preference choice test. Eight males were used as subjects and urine donors and four females were used as donors. Urine was collected several hours before dark by placing the animals in clean plastic tubs until micturition occurred. Urine was collected with a syringe and stored in

sealed glass vials until used 1-4 h later. Syringes and watch glasses were cleaned thoroughly with water and methanol between urine presentation tests (Epple, 1978). To avoid influences of human odor, plastic gloves were used to handle clean watch glasses.

To determine female reproductive stage, cloacal smears were collected daily with cotton swabs dipped in saline; this was smeared on a slide, dried, Giemsa stained (Zarrow et al., 1964), and examined under a microscope to classify the animal as estrous (presence of nucleated and cornified cells) or non-estrous (presence of leukocytes and debris) (Godfrey, 1969; Fadem et al., 1982). The female urine used in olfactory tests was then classified as estrous or non-estrous.

Urine tests consisted of presenting a single male with 0.04 ml of experimental sources in two Syracuse watch glasses (6.6 cm in diameter) in the home cage. Nest boxes, food, and water bowls were removed from the cage and the animal isolated under a clean opaque plastic tub while test glasses were placed 6 cm apart inside the front of the cage. Choice order was assigned randomly to avoid a bias in presentation. After the animal restriction tub was removed, the amount of sniffing at each watch glass (A or B) was verbally spoken into a tape recorder for three min. Tapes were transcribed using a Conus Digital Stopwatch (accurate to 1/100 s) into total amount of time spent sniffing each choice. Two-sided paired t-tests (Dixon and Massey, 1969) were used to test for significant differences in six comparisons performed, each with a sample size of 16. In Test type 1 (control), two clear neutral watch glasses were presented to determine whether the animals had a right or left bias. Test types 2 and 3 determined if male Monodelphis prefer their own species' urine over

some other, or water. Test type 4 determined if male Monodelphis prefer their own urine over that of another conspecific male. Test type 5 determined if males differentially investigate a source based on sex of donor, and the estrous non-estrous comparison (Test type 6) determined whether male Monodelphis can discriminate a female's reproductive condition from urine samples.

Vocalizations were recorded at 9.5 c.p.s. during 30 (3 familiar male-female, 14 unfamiliar male-female, 8 male-male, and 5 female-female) of the test encounters in the neutral arena with a Uher 4000 Report IC tape recorder, with the microphone (Uher M-517) suspended over the middle of the arena about 60 cm above the substrate. Since behavioral observations were being recorded simultaneously, the vocalizing individual could be later identified. Sonagrams of the vocalizations were made with a Kay Elemetrics Sonagraph (Model 7029A) on a wide band pass filter. The sonagrams were classified into vocalization types with duration, frequency, and repetition rate quantified since these parameters are important in determining function in mammalian auditory communication (Eisenberg, 1981). Vocalizations were then classified into the four major syllable types reported for marsupials (Eisenberg et al., 1975). Type I through IV syllables are: tonal, non-aggressive sounds; sounds composed of tonal mixtures with a lot of background content; short repeated sounds less than 0.02 s in duration; and non-harmonic sounds; respectively.

RESULTS

Behavior Description and Overview

A catalogue of 74 behaviors observed in Monodelphis comprise the behavioral catalogue (Table 1). Grooming, resting, and yawning primarily occurred in encounters lacking intense aggression, or after initial social and aggressive contacts had been made.

Exploration was a major component of Monodelphis behavior in which all areas of the substrate and walls of the arena were sniffed and explored. Tongue protrusion occurred, as well as an upright erect sniff where the animal stands on its hind legs balancing itself with its tail. Tongue protrusion by extending the tongue, waving it, and then retracting it was performed by both sexes in all contexts, particularly solitary and dyad encounters.

Attentive stares at conspecifics lasted from 1-30 s. In the dyad pairings, subordinant animals frequently watched dominants and avoided them if approached.

Scent marking behaviors performed by Monodelphis included perineal, metasternal, chin, side, and hip rubs in addition to urination and defecation marking. Sniffs at each of these mark types were recorded and included in scent marking box plots. Males in opposite sex encounters usually sniffed, picked up, and even licked feces of females. Although large amounts of urine could be voided, up to 3 ml, it was usually scat-

tered throughout the arena in tiny visible droplets. Urine dribbling and defecation were usually accompanied by up and down tail movements.

Aggressive behaviors included: following the conspecific, gaping, upright threats, chasing, lunging, biting, and fights. Mouth gaping, varying from slight to wide, was often accompanied by hissing or screeching at the opponent. Upright threats occurred when an animal sat on its haunches while gaping at its opponent. Chasing was performed primarily by females in opposite sex encounters, and by dominant males in male dyads. Lunging at the opponent was performed primarily by females and dominant dyad males and it was generally followed by biting and fighting, or retreating. Most bites were delivered to males by females. Females bit males in 80% of the familiar pairings, but males bit females in only 13% of the encounters. In unfamiliar pairings females bit males in 80% of the encounters, while males bit females in only 25% of the encounters. In same sex dyads males bit each other in 62% of the encounters, while 53% of the female dyads included biting. Fights occurred in 53% of the familiar male-female encounters and in 80% of the unfamiliar male-female encounters. Fighting occurred in 60% of the female dyads and in 86% of the male dyads. Other behaviors associated with dominance and aggression were tail position from horizontal to dragging it on the ground and projecting the ears forward while approaching and threatening.

Retreating occurred in response to approach, aggressive threat, chasing, or fighting. Other retreat associated behaviors associated with subordination were carrying the tail up beyond the horizontal and folding the ears to the side.

Sexual behavior leading to copulation was observed several times. Males emitted a clicking vocalization while pursuing and grasping females and nosing them in the cloacal region. Males bit the nape of the female's neck during copulation (neck gripping) and locked hind legs to hers to keep the female from retreating. Copulations occurred when animals were lying on their right or left sides and alternated between these two postures. No litters were produced as a result of the copulations observed. After ejaculation, both animals extensively groomed, particularly in the genital region.

Neutral Test Encounters

Grooming and Resting

Comparisons between grooming behavior of the four male and four female experimental contexts were significantly different ($X^2 = 20.1$, $p = .0002$; $X^2 = 25.01$, $p = .0001$, respectively) and justify multiple single comparisons (Fig. 1, Table 2). Solitary males groomed significantly more than other male types, while unfamiliar males (of the unfamiliar male-female pairs) groomed the least (Table 2). Familiar males (of the familiar male-female pairs) and dyad males (of the male-male pairings) did not differ significantly. Solitary females groomed and rested significantly more than other female types. Dyad females groomed significantly more than females paired with their male cagemate (familiar females) or females paired with strange males (unfamiliar females); which did not differ. Solitary males and solitary females did not differ; however,

familiar, unfamiliar, and dyad females groomed significantly more than their male counterparts (Table 2).

Exploratory Behavior

Comparisons of defined exploratory behavior within the four male and four female types were both individually significant ($X^2 = 22.2$, $p = .0001$; $X^2 = 45.9$, $p = .0001$, respectively) (Fig. 2, Table 2). Solitary males explored significantly more than all other male types and familiar males explored significantly more than unfamiliar males. No significant differences in exploratory behavior were observed between familiar males and dyad males or between unfamiliar males and dyad males. Solitary females also explored significantly more than all other female types. Dyad females explored significantly more than familiar or unfamiliar females and unfamiliar females explored significantly less than familiar females. There were no differences in exploratory behavior between solitary males and solitary females, familiar males and familiar females, or unfamiliar males and unfamiliar females, but dyad females did explore significantly more than dyad males.

Attentive Behavior

Comparisons within male and within female types showed significant differences within groups ($X^2 = 20.5$, $p = .0001$ for males; $X^2 = 33.8$, $p = .0001$ for females) (Fig. 3, Table 2). Dyad males and dyad females were significantly more attentive than the unfamiliar or familiar pairings. Males in unfamiliar or familiar context encounters did not differ, but

unfamiliar females were more attentive than familiar females. No significant differences occurred due to sex in paired comparisons.

Scent Marking

Comparison of scent marking behavior between male types was significant ($X^2 = 15.5$, $p=.0015$) but was not in females ($p=.07$)(Fig 4, Table 2). Solitary males and unfamiliar males did not differ in scent marking, but both scent marked significantly more than familiar males and dyad males, which did not differ. Dyad females scent marked significantly more than dyad males but there were no other differences in cross sex comparisons.

Vocalizations

Comparisons of vocal activity within male and within female types were significantly different ($X^2 = 20.3$, $p=.0002$, $X^2 = 25.2$, $p = .0001$, respectively) (Fig. 5, Table 2). Familiar males vocalized significantly less than unfamiliar males or dyad males. Familiar females vocalized more than unfamiliar females or dyad females, which did not differ from each other. Comparing between sexes, only familiar females vocalized more than familiar males.

Social Contact

Comparisons of Monodelphis social contact behavior were significantly different within male and within female types ($X^2 = 21.2$, $p = .0001$; $X^2 = 17.0$, $p=.0007$, respectively)(Fig 6). Familiar males exhibited

more social contact behavior than dyad males ($X^2 = 4.69$, $p = .03$). No other significant differences were found.

Aggressive Behavior

There were significant differences in aggressive behavior among male types and among female types ($X^2 = 31.5$, $p = .0001$ for males, and $X^2 = 26.9$, $p = .0001$ for females) (Fig. 7, Table 2). Male dyads were significantly more aggressive than familiar or unfamiliar males which did not differ. Among females, unfamiliar animals exhibited significantly more aggressive behavior than familiar females or dyad females, which were not significantly different from each other. Unfamiliar females exhibited significantly more aggressive behavior than unfamiliar males, but dyad males were more aggressive than dyad females. Familiar males and familiar females did not differ.

Retreat Behavior

Retreat behavior comparisons were significantly different within male and within female types ($X^2 = 17.5$, $p = .0006$; $X^2 = 20.5$, $p = .0001$, respectively) (Fig. 8), but no differences were found in individual comparisons except that unfamiliar males retreated more than unfamiliar females ($N = 38$, $r = 13$, $p = .036$).

Sexual Behavior

There were no significant differences in sexual behavior in either sex in familiar and unfamiliar pairings. (Fig. 9). Unfamiliar males ex-

hibited more sexual behavior than unfamiliar females ($N = 24$, $r = 4$, $p = .001$), but familiar pairs did not differ.

Scent Marking

Perineal Drag

Perineal dragging comparisons within the four male types were statistically significant ($X^2 = 8.27$, $p = .0408$), but were not within female types ($p = .09$) (Fig. 10, Table 3). Solitary males perineal dragged significantly more than other male types. Unfamiliar females and dyad females perineal dragged significantly more than unfamiliar and dyad males. There were no significant differences in perineal dragging between solitary males and females or between familiar male and female pairs.

Dig Perineal Drag

There were no significant differences in dig perineal dragging among female types ($p = .23$, Table 3). Males were never seen performing this behavior and it was infrequent in females.

Metasternal Rub

Overall median test comparisons of metasternal rubbing were not significant within males or within females ($p = .41$ and $p = .52$, respectively), and no significant differences were found between any of the male-female comparisons. Metasternal rubbing was not performed by familiar males or solitary females.

Chin Rub

No significant differences in chin rubbing were found among males ($p=.28$) or among females ($p=.38$)(Table 3). Comparing between sexes showed that unfamiliar males chin rubbed significantly more than unfamiliar females but no other significant differences were noted. Solitary and familiar females did not chin rub.

Side Rub

There were no significant differences within the four male types ($p=.98$), within the four female types ($p=.40$), or in between sex comparisons.

Hip rub

Hip rubbing comparisons within males showed no significant differences while within females showed significance ($X^2 = 9.76$, $p = .021$)(Table 3). Unfamiliar females hip rubbed significantly more than solitary females and familiar females ($X^2 = 5.57$, $p = .018$), but not more than dyad females. There were no significant differences between solitary, familiar, or dyad females. Females hip rubbed significantly more than males in unfamiliar and dyad situations. Males hip rubbed only in dyad encounters.

Urine Dribble

No significant differences in urine dribbling were found among male types or among female types ($p=.12$ and $p=.87$, respectively) (Fig. 11)(Table 3). Both familiar and unfamiliar females urine dribbled sig-

nificantly more than familiar and unfamiliar males. There were no significant differences between solitary males and solitary females or between dyad males and dyad females.

Defecation

Overall defecation comparisons within males and within females were significant ($X^2 = 9.64$, $p = .013$; $X^2 = 11.25$, $p = .011$; respectively)(Fig. 12)(Table 3). Solitary males defecated significantly more than any other male type, while there were no differences between other male types. Solitary females defecated significantly more than familiar or unfamiliar females, but not more than dyad females. Familiar, unfamiliar, and dyad females did not differ from each other. Females defecated significantly more than males in the solitary ($X^2 = 5.06$, $p = .026$), unfamiliar, and dyad encounters; but there was no difference between familiar males and familiar females.

Vocalizations

Clicking

Comparisons of bouts of clicking within the 30 min encounters among female types were significant ($X^2 = 15.32$, $p = .0005$), but were not significant among males ($p = .08$)(Fig. 13, Table 4). Dyad females clicked significantly more than other female types. Unfamiliar males clicked significantly more than unfamiliar females while familiar males and females, and dyad males and females did not differ.

Hissing

The frequency of hissing vocalizations within male types was significantly different ($X^2 = 16.94$, $p = .0002$), but was not so for females ($p = .49$)(Fig. 14, Table 4). Unfamiliar males hissed significantly more often than familiar males and dyad males hissed significantly more than other male types. The between sex comparisons showed that familiar females hissed significantly more than familiar males, but there were no differences in hissing between males and females in unfamiliar or dyad contexts.

Screeching

Comparisons of frequency of screeching during the 30 min encounters among male and female types were significant ($X^2 = 7.6$, $p = .02$ and $X^2 = 16.88$, $p = .0002$, respectively)(Fig. 15, Table 4), but no significant difference was found in screeching between familiar and unfamiliar males. Screeching occurred more often in dyad males than unfamiliar males, but not more than familiar males. Familiar females screeched significantly more than unfamiliar and dyad females who also were significantly different. When comparing between sexes, both familiar and unfamiliar females screeched significantly more than their respective males, but dyad males screeched significantly more often than dyad females.

Squawking

An overall comparison of frequency of squawking vocalizations among male types was significant ($X^2 = 12.02$, $p = .0025$), but was not among

females ($p = .59$)(Table 4). Dyad males squawked significantly more than unfamiliar males. No other significant differences were found.

Chittering

Comparisons of chittering frequency during the 30 min encounters within males were not significant ($p = .11$), but were for females ($X^2 = 21.95$, $p = .0001$)(Table 4). Familiar females chattered significantly more than either unfamiliar females, dyad females, or familiar males. No significant differences in chittering were found between unfamiliar pairs or dyads. Familiar males, dyad males, and dyad females did not produce the chittering vocalization.

Social Contact

No significant differences were found within male or female types in approaching, nose to nose, nose to head, nose to neck, nose to rump, or circling behavior.

Nose to back

An overall comparison of nose to back behavior was significant within males and within females ($X^2 = 10.4$, $p = .0055$ and $X^2 = 7.3$, $p = .026$, respectively)(Fig. 16, Table 5). Familiar and unfamiliar males did not differ, but both exhibited significantly more nose to back behavior than dyad males. There was no significant difference between familiar and unfamiliar females, and both exhibited significantly more nose to back

contact than dyad females. There were no differences in the between sex comparisons.

Nose to side

Nose to side social contact behavior was significantly different in male types but not females ($X^2 = 8.4$, $p = .015$ and $p = .08$, respectively)(Table 5). Familiar and unfamiliar males exhibited significantly more nose to side contact behaviors than dyad males, but they did not differ from each other. Comparing between sexes showed only that unfamiliar females exhibited significantly more nose to side contact behavior than unfamiliar males.

Nose to abdomen

Nose to abdomen contact behavior did not differ within male and female types ($p=.69$ and $p=.23$, respectively). Unfamiliar females exhibited more of this contact behavior than unfamiliar males ($N=5$, $r=0$, $p=.031$).

Nose to cloaca

Comparisons of nose to cloaca contact behavior were significant among males and among females ($X^2 = 26.82$, $p = .0001$ and $X^2 = 15.44$, $p = .0004$, respectively)(Fig. 17, Table 5). Within male pair types, familiar and unfamiliar individuals exhibited significantly more nose to cloaca contact than did dyad males. Unfamiliar females displayed significantly more nose to cloaca contact than dyad females, but familiar females did not differ from either unfamiliar or dyad females. Familiar and unfa-

miliar males exhibited significantly more nose to cloaca behavior than familiar or unfamiliar females, but dyad males and females did not differ.

Nose to tail

Nose to tail contact behavior comparisons within male types were significant ($X^2 = 9.76$, $p = .007$), but were not among females ($p = .38$). Familiar males displayed more nose to tail contact behavior than dyad males ($X^2 = 4.01$, $p = .045$). There were no other differences within or between sexes.

Dominance-Subordinance Comparisons

Dominance-subordinance relationships were noted in dyad encounters. Within the 21 male dyad encounters, dominance-subordinance relationships could be classified for 20 encounters, while 16 of 20 female encounters could be so classified. These data are presented from neutral test encounters by major behavior categories, and for the individual behavior components of scent marking, vocalizations, and social contact.

Neutral Test Encounters

In dominant-subordinant relationships, dominant males exhibited more social contact while subordinant males vocalized more (Table 6). Dominant males were more aggressive than subordinants which retreated when pursued by dominant males (Fig. 18, 19; Table 6). There were no significant differences between dominant and subordinant males with respect to grooming, exploration, attention, or scent marking.

Dominant females scent marked and exhibited significantly more social contact behavior than subordinate females. Subordinate females were more attentive than dominant females and retreated more (Fig. 19). There were no significant differences in grooming, exploration, vocalizations, or aggression between dominant and subordinate females.

Dominant males were significantly more aggressive than dominant females which groomed, explored, and scent marked more. Dominant males and dominant females did not differ in attentive behavior, vocalizations, social contact, or retreating (Table 6).

Subordinate females groomed and explored significantly more than subordinate males, while subordinate males retreated more. There were no significant differences between subordinate males and females with respect to attention, scent marking, vocalizations, social contact, or aggression.

Scent marking

Dominant males chin rubbed significantly more than subordinate males, which defecated more than dominants (Table 7A). Dominant females perineal dragged, hip rubbed, and defecated significantly more than subordinate females and dominant males, but there were no differences in chin rubbing behavior. No differences were found between subordinate males and subordinate females. Dominance-subordinance comparisons showed no significant differences in dig perineal dragging, metasternal rubbing, side rubbing, or urine dribbling.

Vocalizations

Subordinate males clicked and screeched significantly more than dominant males (Table 7B). No other significant differences were found.

Social Contact

Dominant males approached and exhibited more nose to rump behavior than subordinate males, but did not differ in nose to nose behavior (Table 7C). Dominant females approached more and exhibited more nose to nose behavior than subordinate females, but did not differ in nose to rump behavior. There were no significant differences in any social contact behaviors between dominant males and females or between subordinate males and females. Additionally, no significant differences were found in the following behaviors: nose to head, nose to neck, nose to back, nose to side, nose to abdomen, nose to cloaca, nose to tail, and circling (Table 7C).

Preference Tests

When presented two neutral watch glasses (control), male Monodelphis showed no directional bias in sniffing of right vs. left watch glasses (Paired t-test, $t=1.85$, $p>.05$).

Male Monodelphis presented with urine of another male Monodelphis or that of an adult male laboratory mouse (Mus musculus), urine of another male Monodelphis or distilled water, or other male Monodelphis urine versus their own urine did not differ significantly in amount of time associated with either source. When males were presented non-estrous

conspecific female urine vs. conspecific male urine, males sniffed female urine statistically most often ($t=2.82$, $.01 < p < .02$). When presented conspecific non-estrous vs. estrous urine, estrous female urine was sniffed significantly more than non-estrous urine ($t=2.21$, $.02 < p < .05$).

Sonographic Vocalization Analysis

Clicks were short (3.41 ms duration for males and 2.41 ms for females) sounds (4.4-13.6 kHz) produced by males as contact promoting behavior while attempting to approach females in a sexual context and also by both sexes in submissive contexts while retreating (Table 8). Intervals were short and were nearly constant within a bout. Clicks are classified as Type III syllables (Eisenberg et al., 1975) since durations are less than .02 s and are always repeated in a bout (Fig. 20).

Hissing was often seen in agonistic encounters with another individual. Hisses were not generally repeated in a series and are classified as Type IV sounds (Eisenberg et al., 1975) since no tonal structure was noted in this vocalization (Table 8)(Fig. 21). Hisses were low intensity sounds generally less than 5 kHz which were accompanied with gaping of the mouth as an offensive or defensive threat.

Squawking was also an agonistic vocalization and was not generally repeated in a bout. The major components were generally below 4 kHz although less audible components may be as high as 12 kHz (Table 8). Squawks had a more sudden onset than hisses, but were not as abrupt as screeches and were classified as Type II sounds (Fig. 22).

Screeches were also agonistic vocalizations produced by Monodelphis and consisted of sudden onsets with most of the energy concentrated between 1 and 14 kHz (Table 8). Mean maximum frequency could not be calculated due to limitations of the recording equipment, but maximum frequency of the principle components was around 16 kHz, with harmonic components above this. Screeches were produced singly or in succession depending on the social context. Because of the harmonic nature of screeches and short duration (<.06 s), screeches are classified as short Type II syllables (Eisenberg, et al., 1975) (Fig. 23).

Chattering, an uncommon vocalization, was a series of "screech-like" components occurring in rapid succession with a mean interval of about .005 s and was generally emitted in an agonistic context (Table 8). Each "screech-like" component usually lasted less than half as long as a normal screech. Frequencies ranged up to around 16 kHz, but an exact maximum could not be determined because of equipment limitations; however, as with screeches, the principal component was at a maximum around 16 kHz, with harmonics above this. Like screeches, chitters are classified as Type II short syllables (Fig. 24).

DISCUSSION

The behavioral catalogue for Monodelphis domestica consisted of 74 behaviors which grouped into nine behavioral categories, most of which are also found in other members of the Didelphidae (Hunsaker and Shupe, 1977; Streilein, 1982f).

Grooming and resting postures were common in solitary situations and in dyad female pairings where aggression was low. Females groomed more than males in every situation except when solitary. In male-female encounters and male-male encounters grooming and resting behaviors were reduced as sexual or agonistic interactions increased. Grooming behavior increased after initial social and aggressive contacts had occurred. Grooming modes observed in encounters with Monodelphis (hind foot scratching, face washing, and genital grooming) were typical of those generally reported for mammals (Eisenberg, 1981), and were essentially the same as in Didelphis marsupialis (McManus, 1970). Saliva spreading during grooming reportedly serves to clean the fur, and it may also serve a chemical communicatory function (Eisenberg and Kleiman, 1972).

Exploring was characterized by movement around the enclosure sniffing substrates and the air. Solitary individuals explored the arena more than paired animals while female pairs, which were characterized by low agonistic levels explored somewhat less. Unfamiliar male-female pairs, which exhibited extensive sexual and agonistic interactions, explored the least. Monodelphis prey on small invertebrates and vertebrates in the ground litter (Streilein, 1982a), so extensive exploratory behavior such

as digging and burrowing would be associated with locating food. Exploration in Monodelphis is similar to that reported for terrestrial Didelphis (McManus, 1970).

Tongue protrusion, exhibited primarily by solitary individuals and dyad pairs, may be involved in vomeronasal organ function. These structures have been reported in didelphids (Barnes, 1977; Hunsaker and Shupe, 1977), and probably enhance sensory abilities. Monodelphis may be unique in that tongue protrusion has not been previously reported from any other didelphid. The probable occurrence of this additional sensory ability in Monodelphis further demonstrates the major importance placed on olfactory communication in this nocturnal species.

Scent marking by Monodelphis commonly occurred during exploration of new environments. Scent marks would permit an individual to move through the area along a familiar pathway and could also enable individuals to locate the presence of conspecifics (Johnson, 1973). The dominance-subordinance relationship is one factor which influenced scent marking frequency. Typically dominant mammals scent mark more frequently than subordinants, (Johnson, 1973; Ralls, 1971), and this is true for female Monodelphis, but not for males. Dominant male Monodelphis which exhibited high agonistic levels toward subordinants, scent marked less frequently than females. Paired female encounters were not characterized by high levels of agonistic behavior, and therefore more time could be spent scent marking. Scent marking was also involved in sexual aspects of Monodelphis behavior. Males paired with unfamiliar females scent marked more frequently than when paired with familiar females or with other males. Since Monodelphis are intolerant of conspecifics

(Streilein, 1982e), and are therefore probably solitary animals, males should investigate the reproductive status of every female encountered in order to maximize their reproductive fitness by breeding with all receptive females.

Only dyad male Monodelphis marked less frequently than dyad females and this may have been related to degree of aggression. Monodelphis is unusual among mammals in that males and females scent marked with equal frequency (Johnson, 1973; Thiessen and Rice, 1976; Blaustein, 1981). Solitary male or female Monodelphis perineal dragged frequently, suggesting that this behavior serves to familiarize the habitat and to advertise an individual's presence to conspecifics. Streilein (1982f) observed occasional perineal dragging by male Monodelphis but did not assign a function to this behavior. From my study, female Monodelphis perineal dragged more than males when in unfamiliar pairing contexts. Trupin and Fadem (1982) reported that receptive female Monodelphis perineal drag and postulated a function of female sexual advertisement. In this study, both sexes perineal dragged, including non-receptive females. Dominant female Monodelphis perineal dragged more frequently than subordinate females, suggesting that it may be a dominance-related behavior. Perineal dragging served for both sexes to mark the habitat for familiarization, and for female sexual advertisement.

Dig perineal dragging moves the substrate via the foot motion across the perineal region and was exhibited only by female Monodelphis, and has not been described for any other didelphid.

Prominent metasternal glands, which produced a strong glandular odor, were present in Monodelphis and were used by both sexes.

Metasternal marking was observed in all contexts except for familiar males and solitary females. Trupin and Fadem (1982) reported that only male Monodelphis metasternal rubbed during interactions with females, but in my study females also metasternal rubbed when paired with females or males. In comparison, metasternal rubbing by Marmosa robinsoni is restricted to dominant males marking their habitat (Hunsaker and Shupe, 1977).

In unfamiliar male-female contexts, male Monodelphis chin rubbed more than females suggesting that it may serve in precourtship, or as a male identification mark. Chin rubbing was the only marking mode in which dominant males marked more than subordinant males, which suggests its use as a dominance identification mark. Trupin and Fadem (1982) observed male Monodelphis chin rubbing in male-female interactions where males re-marked sites marked by other males. This apparently occurred because their arena was not sanitized between trials. Chin rubbing is reported to be an important marking mode among marsupials and insectivores (Eisenberg and Kleiman, 1972).

Lateral side rubbing occurred in all contexts and was used by both sexes which suggests it was a general marking behavior. Trupin and Fadem (1982) reported side rubbing only for male Monodelphis during male-female interactions. This mode of marking has not been reported for any other member of the Didelphidae and it occurred in this study as a very general marking behavior. Monodelphis hip rub by pulling the body forward with the forelegs while dragging the hip over the substrate. This mode of marking by females occurred in unfamiliar encounters, and dominant females hip rubbed often. This was less frequently observed in dominant

males and suggests that hip rubbing was primarily a female behavior and related to dominance in Monodelphis. However, Trupin and Fadem (1982) observed hip rubbing in receptive female Monodelphis — so it might also serve in mate attraction.

Urine droplets were sniffed by conspecifics and they frequently licked at urine droplets. Females urine dribbled more often than males in familiar and unfamiliar contexts which suggests that it was a sexual condition advertisement behavior. Preference association tests conducted with urine showed that male Monodelphis can distinguish female urine donors when in estrus or anestrus, but males did not discriminate among other sources of urine. It would be advantageous for male Monodelphis to recognize female Monodelphis urine to be aware of her presence in the locality permitting him to pursue the female when in estrus. Recognition of other male conspecifics may be by other scent marks rather than urine.

Monodelphis frequently defecated during encounters, and males always investigated feces, suggesting a potential role in chemical communication. Information being transmitted may be in the feces or may have originated from anal gland secretions on the feces (Eisenberg, 1981). Solitary animals defecated more than paired animals, perhaps because they were not interacting with conspecifics. Females defecated more than males in all contexts, except in familiar pairings, where familiarity may have reduced the importance of this form of communication. Defecation was greater for subdominant males than dominant males, but the reverse was true for dominant and subdominant females. Defecatory behavior varied widely with social context and sex, thus making generalizations difficult.

A qualitative scheme of behavior and vocalization types has been reported for Didelphis (McManus, 1970; Hunsaker and Shupe, 1977). Vocalizations in Monodelphis appeared to be graded similarly to the didelphid scheme except for the substitution of squawks for growls, with the latter not being emitted by Monodelphis. Click vocalizations in Monodelphis functioned in submissive contexts as well as when males approached females in a sexual context. Chittering was difficult to assign a function to as it occurred at low frequency, but could serve as a low level threat. Vocalizing occurred in all paired Monodelphis encounters and vocalizations included the click, hiss, squawk, screech, and chitter. In familiar pairings where aggression was reduced, familiar male Monodelphis vocalized the least while familiar female Monodelphis vocalized the most. Because of familiarity, females may have substituted vocalization threats for overt aggression. Indeed, screeching, the most intense vocalization, was emitted more frequently by familiar than by unfamiliar females. Subordinate males vocalized more than dominant males and vocalizing appeared to be a defensive threat. Subordinate animals who were retreating from dominants screeched more and emitted more clicks than dominants did.

Clicks, Type III syllable vocalizations (Eisenberg et al., 1975), were used in submissive and courtship contexts and were close contact vocalizations that were easily produced and located. These vocalizations are widespread in mammalian groups (Gould, 1983). Clicks were emitted by male Monodelphis pursuing females, and in submissive contexts by either sex while retreating. Trupin and Fadem (1982) report only male clicks; however, in my study, submissive females did produce the clicking

vocalization when paired with either unfamiliar males or dominant females. Didelphis clicks are similar to Monodelphis clicks, but emission intervals are longer, while those in Marmosa are longer in duration, lower in frequency, and occur more frequently than Monodelphis clicks (McManus, 1970; Eisenberg et al., 1975).

Hisses, Type IV syllables were characterized by Eisenberg et al., (1975), as low intensity aggressive vocalizations, and were frequently emitted during Monodelphis encounters. Male hissing appeared to increase with increasing agonistic levels from the least agonistic familiar situation to the most agonistic dyad pairings.

Squawk vocalizations, also Type IV syllables (Eisenberg et al., 1975), were not repeated and were most frequent in dyad male encounters where they were emitted principally during fights.

Screeches are Type II syllables (Eisenberg et al., 1975), and were characterized as high intensity agonistic vocalizations for didelphids (Hunsaker and Shupe, 1977). Screeches were the most common Monodelphis vocalization recorded. Familiar females screeched more and those vocal threats appeared to replace active aggression. Screeches were also common in the highly agonistic dyad male encounters. Trupin and Fadem (1982) reported a spitting vocalization emitted by sexually non-receptive female Monodelphis toward pursuing males, and this was characterized as a screech vocalization in my study. Didelphis screeches differ from Monodelphis as they are longer in duration (700 to 1000 ms), and have major frequency components between 2 and 15 kHz, and are primarily produced during male-male interactions (McManus, 1970).

Chitter vocalizations were rarely heard and were characterized as a rapid series of screech components, which were classified as Type II syllables (Eisenberg et al., 1975). Chittering was emitted by males primarily when paired with strange females and by females paired with either familiar or unfamiliar males. Chitters were seldom produced and were emitted most frequently by familiar females toward cagemate males and it may function as a low level threat. Chittering has not been previously described for other didelphids.

Social contact behaviors characterized by approaches, directed sniffs, or body contacts with a conspecific were more important in male-female contexts. Males sniffed the cloacal region of females more frequently, enabling them to assess female reproductive status. Females frequently sniffed at the male side and abdomen, but both sexes sniffed at each others backs. Such olfactory and tactile contacts facilitate sexual behavior as Trupin and Fadem (1982) had previously observed in male-female Monodelphis interactions preceding copulation. Social contact behaviors are important within sex contacts, particularly when dominant members approached subordinants and initiated social contact. Dominant males approached and sniffed subordinate males at the nasal, posterior rump and tail region; while dominant females approached and sniffed at the subordinate female's anterior nasal region. Dominant individuals initiated social contact behaviors with subordinate individuals who then frequently threatened and retreated.

Aggressive behavior was common in Monodelphis encounters where individuals were typically intolerant of conspecifics. Aggressive behavior was greatest in male dyads, but unfamiliar females were also quite ag-

gressive toward males. Female Monodelphis are intolerant of males except when in estrus (Trupin and Fadem, 1982); however, in familiar male and female pairs aggression was reduced, but encounters still displayed non-social agonistic behavior. Levels of aggression differed between dominant and subordinate males but not between females. Therefore in females, dominance must have been assessed other than through aggressive interaction, and it appeared that this relationship was maintained by a tendency to retreat on the part of subordinate females. Indeed, dominance-subordination relationships are often maintained by the continued submissiveness of the subordinate animal (Kaufmann, 1983). Dominant females approached subordinate females and initiated social contact while subordinates retreated. Agonistic behaviors in Monodelphis ranged from following the conspecific, to gaping, upright threat, chase, lunge, bite, and fights. Hiss, squawk, and screech vocalizations frequently occurred with these aggressive behaviors. The basic agonistic repertoire has been qualitatively reported in other members of the Didelphidae (McManus, 1970; Hunsaker and Shupe, 1977; Eisenberg and Golani, 1977). In addition to these aggressive behaviors, dominant Monodelphis also carried the tail low to the substrate and often dragged it. This may serve to draw less attention to the hairless unprotected tail. Since agonistic behavior was apparent in all encounter contexts one could conclude that Monodelphis was a solitary species intolerant of conspecifics, and this has been described as the general pattern for didelphids (Hunsaker and Shupe, 1977; Charles-Dominique, 1983). This would imply that many of these species although reported to be non-territorial may have some short term home ranges and territories.

Behaviors associated with subdominant individuals included fleeing from an opponent, folding the ears back, and elevating the tail. Retreating occurred in response to approaches, threats, or after fights. Subordinates of either sex retreated from dominant individuals, and produced a clicking vocalization which may have functioned as a submissive signal.

Sexual behavior was observed in male-female Monodelphis encounters and included grasping each other with the forelegs, male mounting, and biting the nape of the female's neck during copulation. Clicking vocalizations were emitted by males while following females and initiating sexual behavior. Female Monodelphis were receptive to males only for about 36 hours every 28 days (Fadem et al., 1982), and always repelled male sexual advances with aggressive threats or bites during non-receptive periods. Breeding behavior as described for Monodelphis by Trupin and Fadem (1982) agrees with this study except Trupin and Fadem did not observe males biting the nape of the female's neck during copulation as was observed here and as has been reported to occur in other didelphids (Hunsaker and Shupe, 1977). Copulatory behavior of Monodelphis was also similar to that of Didelphis (Reynolds, 1952; McManus, 1970); and Marmosa (Barnes and Barthold, 1969), except male Monodelphis do not exhibit prolonged intromission periods and they copulate on the ground.

In summary, this study has shown that Monodelphis domestica is a non-social species with frequent agonistic behavior in conspecific interactions, even after the animals have been co-caged for at least two weeks. This non-social behavior has also been described for other members

of the opossum family. Didelphids have been classified as solitary animals with each individual maintaining a home range, but not defended territories (Hunsaker and Shupe, 1977; Charles-Dominique, 1983). Solitary animals in my study spent most of the time grooming, resting, exploring, and scent marking the arena. Scent marking functioned to familiarize the habitat to the individual, and as an identity signpost to other conspecifics. Male Monodelphis could determine from a urine dribble the sex of the individual and if a female, whether she was in estrus or not. Male discrimination of female urine would be important for mate acquisition since males must locate females and determine their sexual condition, and estrus only lasts 36 h each month (Fadem et al., 1982). This study showed that males sexually investigated females by following, rump grasping, sniffing the rump and cloaca; and then proceeded with mounting behavior if the female was receptive. Male Monodelphis domestica should never exhibit a period of diminished sexual drive since females in the caatinga of Brazil cycle year round (Streilein, 1982c). Monodelphis conspecific interactions were agonistic except preceding and during mating — which is similar to that reported for other didelphids (Hunsaker and Shupe, 1977). Non-receptive females were highly aggressive toward males, which usually retreated when aggressively attacked.

Interactions between same sex conspecifics resulted in behavior leading to the determination of dominance and subordination. Male-male encounters exhibited the most aggressive behavior, and this might function to permit dominant males reproductive access to all females in the area. All highly aggressive interactions could also be related to competition for dispersed food resources clumped into the more mesic,

defensible rocky outcrops. Competition among reproducing females for nest sites may also result in aggressive conspecific behavior. Likewise, females should be aggressive to males except when in estrus and requiring insemination for the production of young.

Comparing Monodelphis domestica behaviors to other didelphid species shows some similarities and some differences. Scent marking behaviors common to some didelphids are: perineal dragging, chin rubbing, and urine dribbling. Perineal dragging has been reported for Marmosa robinsoni (Eisenberg and Golani, 1977), and Didelphis marsupialis (McManus, 1970) — which possess anal sacs and proctodeal glands (Müller-Schwarze, 1983). Perineal dragging would be an effective marking mode for a terrestrial mammal such as Monodelphis or an arboreal mammal such as Marmosa since the perineum could be easily rubbed on terrestrial substrate or branches. Rubbing of the chin has also been observed in Didelphis, where males marked the backs of females, and also in Marmosa (Eisenberg and Golani, 1977). Urine dribbling was commonly performed by Monodelphis and was also observed in Marmosa (Eisenberg and Golani, 1977) and Didelphis (McManus, 1970), but McManus did not observe any obvious reaction toward conspecific urine drops in Didelphis. Monodelphis may exhibit more scent marking modes because of its terrestriality as Didelphis and Marmosa are partially to completely arboreal. Metasternal rubbing is also performed by Marmosa (Hunsaker and Shupe, 1977), but hip rubbing was unique to Monodelphis. Hip rubbing would be nearly impossible to perform in an arboreal habitat.

Vocalizations in Didelphis involve four main forms (McManus, 1970). Hissing, growling, and screeching have been ranked with increasing de-

grees of agonistic threat (Hunsaker and Shupe, 1977). Marmosa do not growl and screech, but do have several grades of hissing (Eisenberg et al., 1975). Monodelphis lack the growl, but occasionally use a squawking vocalization in aggressive interactions. Males of all three of these didelphid species click when approaching a female in a sexual context (Eisenberg and Golani, 1977), but Monodelphis is unique in that subdominant individuals of both sexes also click in a submissive re-treating context. The chittering vocalization which Monodelphis also produced has not been described for any other didelphid.

Social contact behaviors common to Monodelphis, Didelphis, and Marmosa are nose to nose contact, nose to cloaca contact, and circling (Eisenberg and Golani, 1977). These are all major forms of contact leading to reproduction, as males and females sniff and examine each other. Monodelphis may exhibit more social contact behaviors not because it is more advanced than Didelphis or Marmosa, but perhaps may be due to its almost entirely terrestrial habits while the other two are somewhat to strictly arboreal. Nevertheless, Monodelphis domestica does have a larger behavioral repertoire than other species of didelphids which have been previously studied.

In conclusion, the behavior of Monodelphis, a non-social nocturnal mammal, is seen to vary in different social contexts. Behaviors and communication patterns have been related to its ecology and reproduction. Olfactory and auditory communication modes were seen to be quite important to the biology of this species. Comparisons to other didelphids show some similarities as well as several new behaviors unique to Monodelphis domestica.

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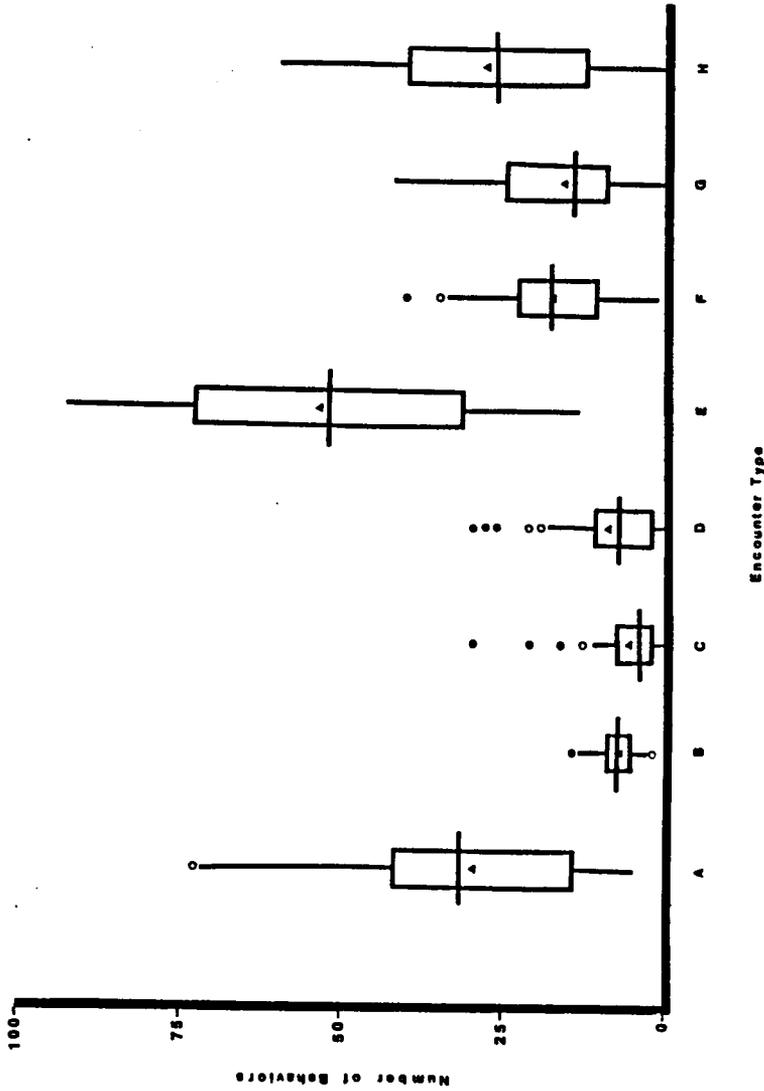


Figure 1. Grooming and resting behavior box plots. A = solitary males (n = 14), B = familiar males (of the familiar male-female pairings) (n = 15), C = unfamiliar males (of the unfamiliar male-female pairings) (n = 40), D = dyad males (of the male-male pairings) (n = 42), E = solitary females (n = 14), F = familiar females (of the familiar male-female pairings) (n = 15), G = unfamiliar females (of the unfamiliar male-female pairings) (n = 40), H = dyad females (of the female-female pairings) (n = 40). The box contains the central 50% of the observations with 25% falling on each side of the median line. Vertical lines extending from the box denote the ranges, open circles denote mild outliers, closed circles denote extreme outliers, and triangles denote means.

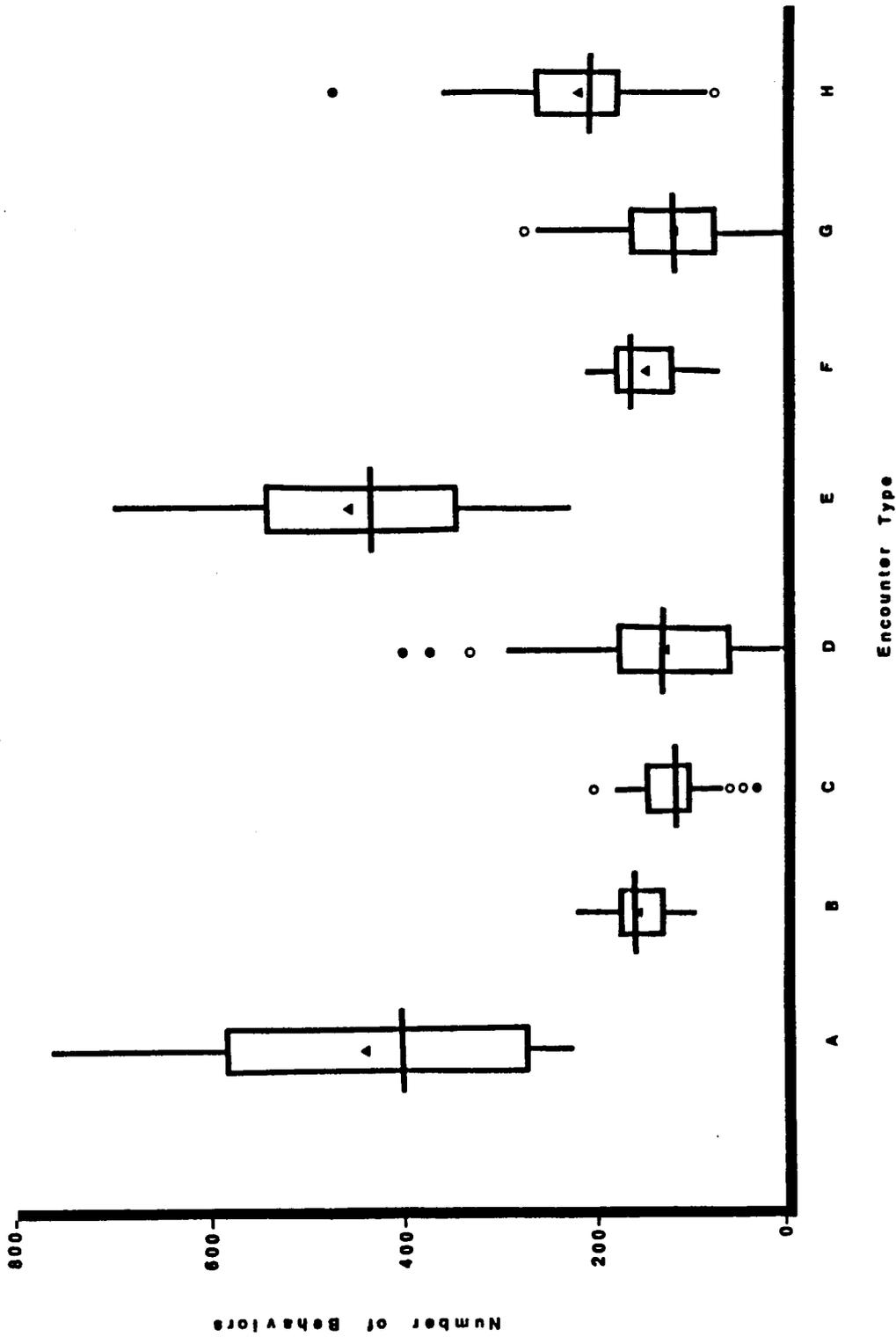


Figure 2. Exploratory behavior box plots. See Figure 1 for explanation.

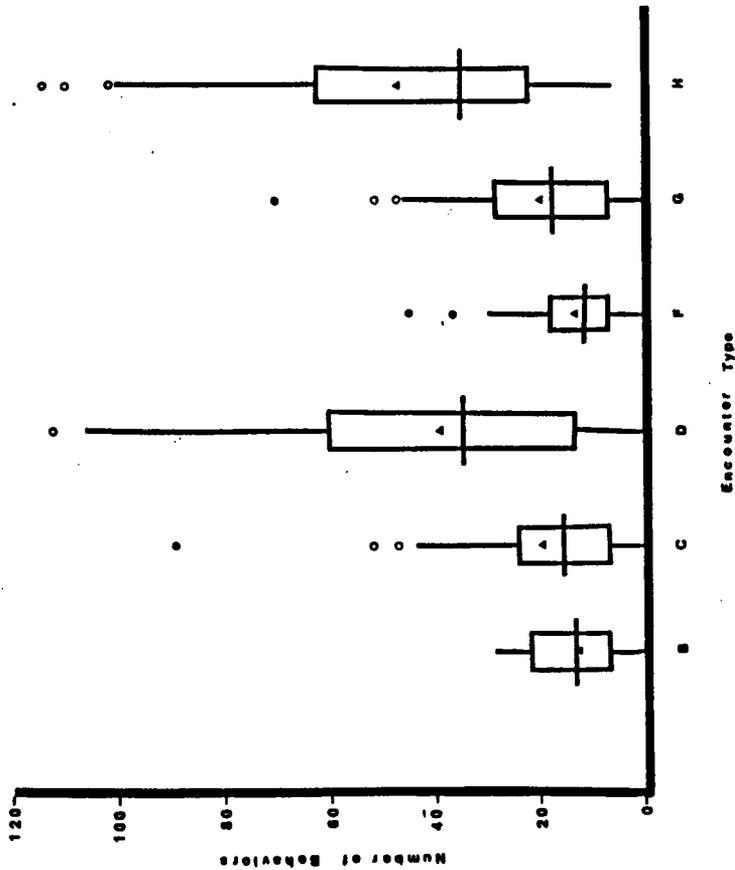


Figure 3. Attentive behavior box plots. B = familiar males (of the familiar male-female pairings) (n = 15), C = unfamiliar males (of the unfamiliar male-female pairings) (n = 40), D = dyad males (of the male-male pairings) (n = 42), F = familiar females (of the familiar male-female pairings) (n = 15), G = unfamiliar females (of the unfamiliar male-female pairings) (n = 40), H = dyad females (of the female-female pairings) (n = 40). The box contains the central 50% of the observations with 25% falling on each side of the median line. Vertical lines extending from the box denote the ranges, open circles denote mild outliers, closed circles denote extreme outliers, and triangles denote means.

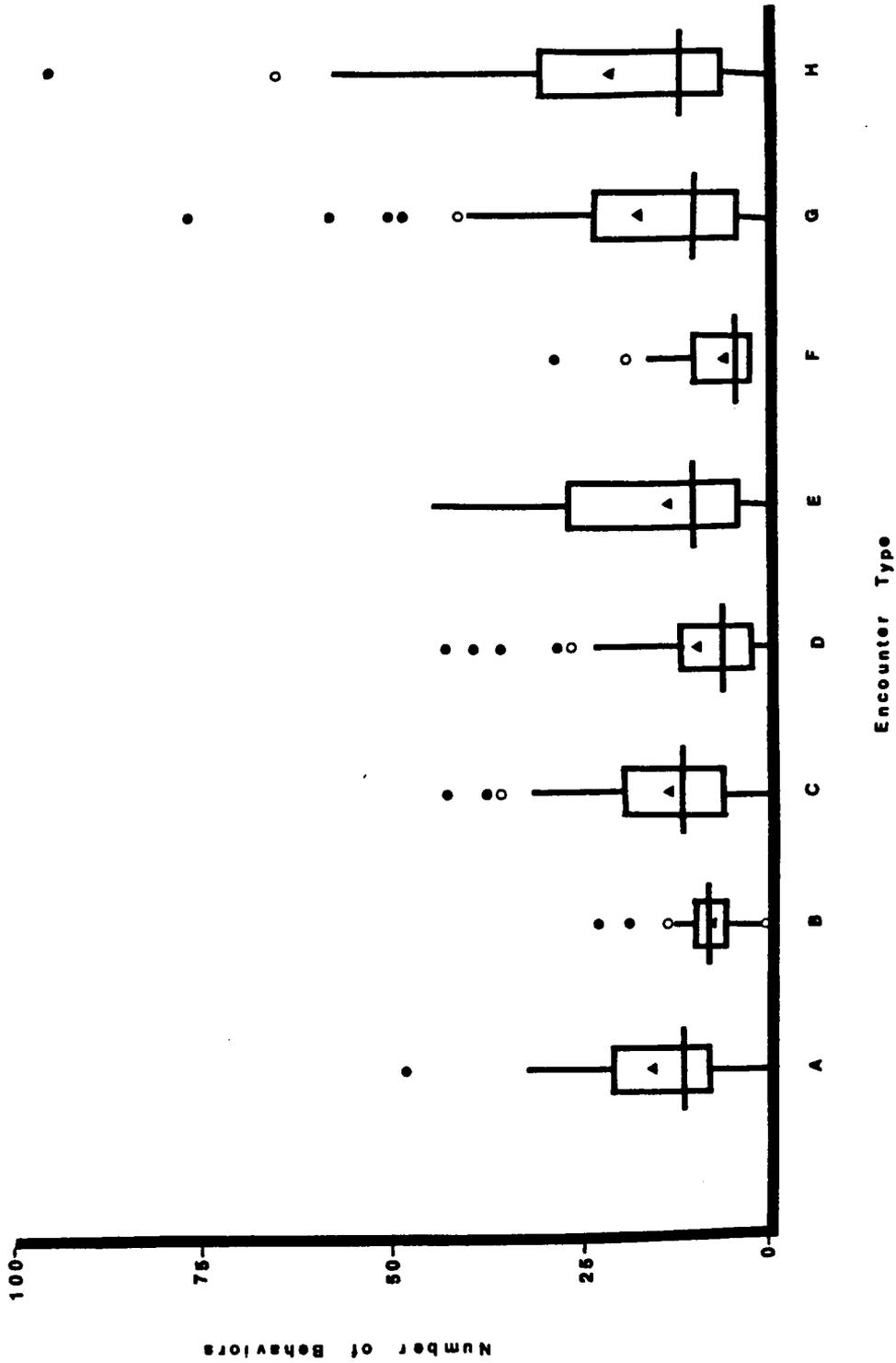


Figure 4. Scent marking box plots. See Figure 1 for explanation.

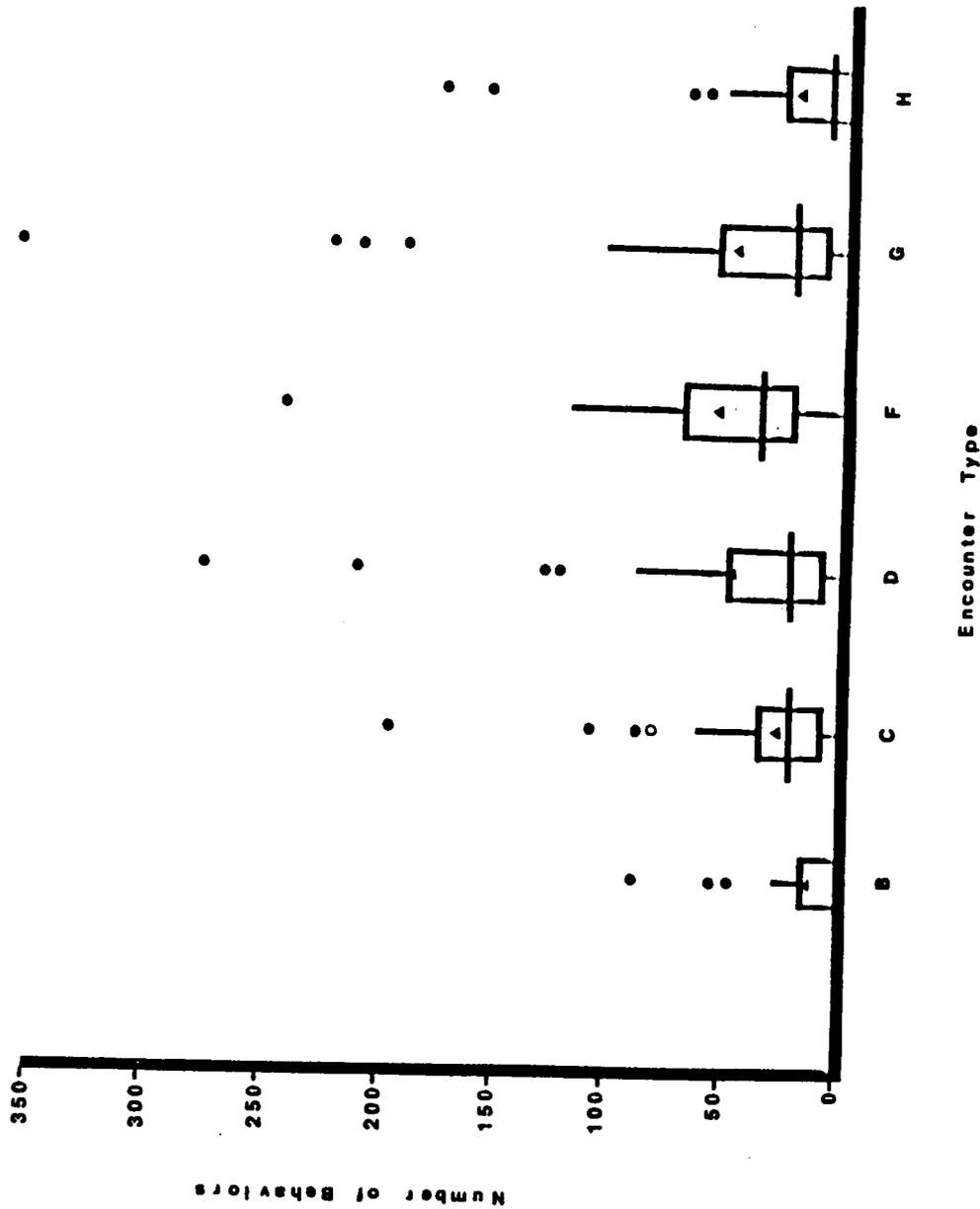


Figure 5. Vocalization box plots. See Figure 3 for explanation. Box plots lacking a visible median line had a median of zero.

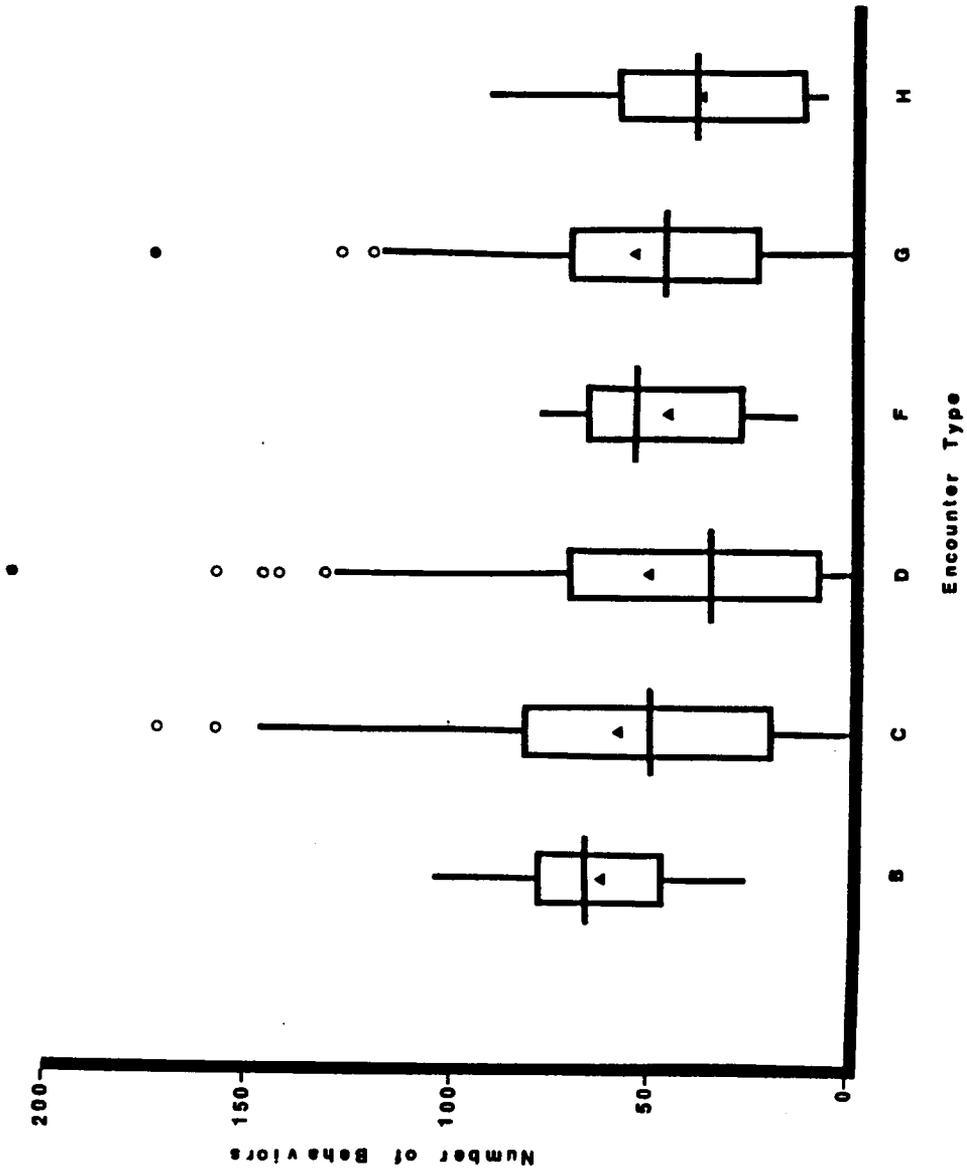


Figure 6. Social contact behavior box plots. See Figure 3 for explanation.

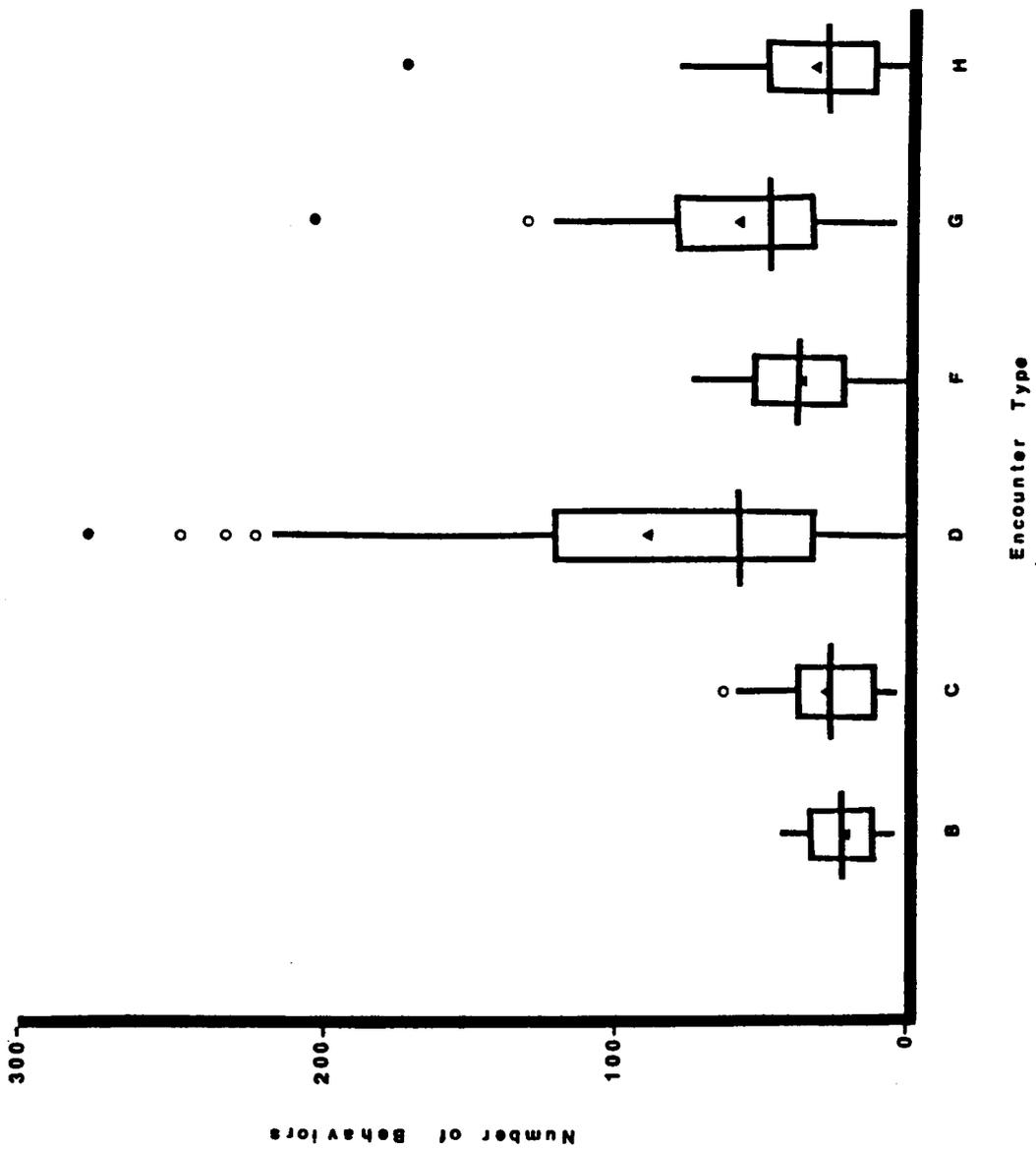


Figure 7. Aggressive behavior box plots. See Figure 3 for explanation.

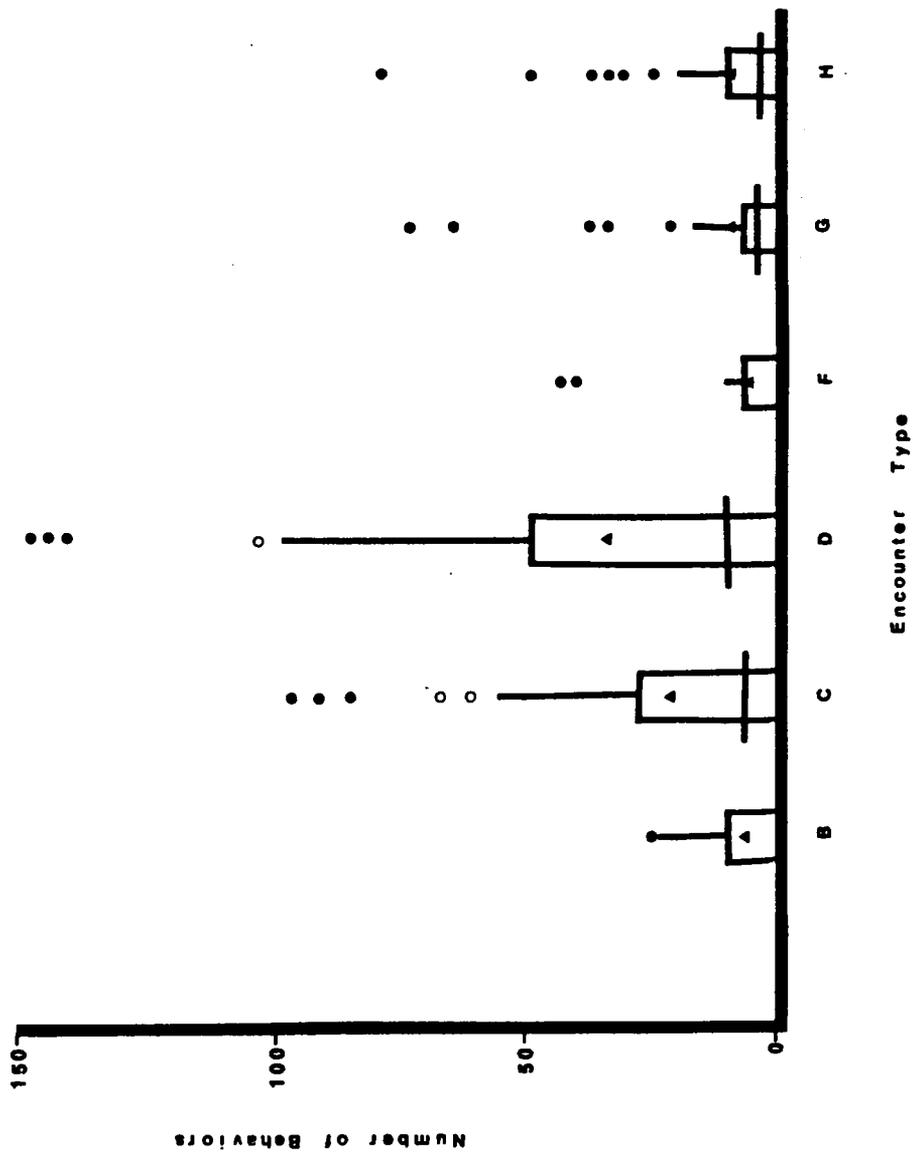


Figure 8. Retreating behavior box plots. See Figure 3 for explanation. Box plots lacking a visible median line had a median of zero.

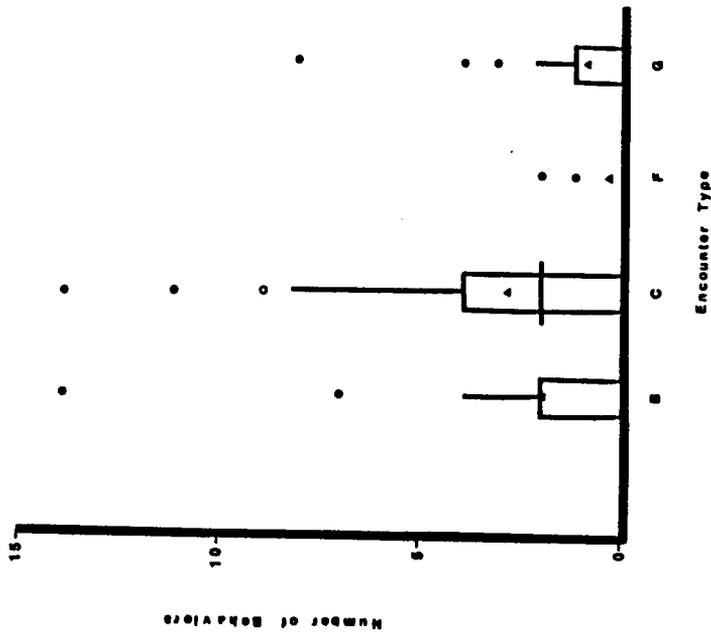


Figure 9. Sexual behavior box plots. B = familiar males (of the familiar male-female pairings) (n = 15), C = unfamiliar males (of the unfamiliar male-female pairings) (n = 40), F = familiar females (of the familiar male-female pairings) (n = 15), G = unfamiliar females (of the unfamiliar male-female pairings) (n = 40). The box contains the central 50% of the observations with 25% falling on each side of the median line. Vertical lines extending from the box denote the ranges, open circles denote mild outliers, closed circles denote extreme outliers, and triangles denote means. Box plots lacking a visible median line had a median of zero. Box plots were absent and only outliers appeared where most observations had values of zero.

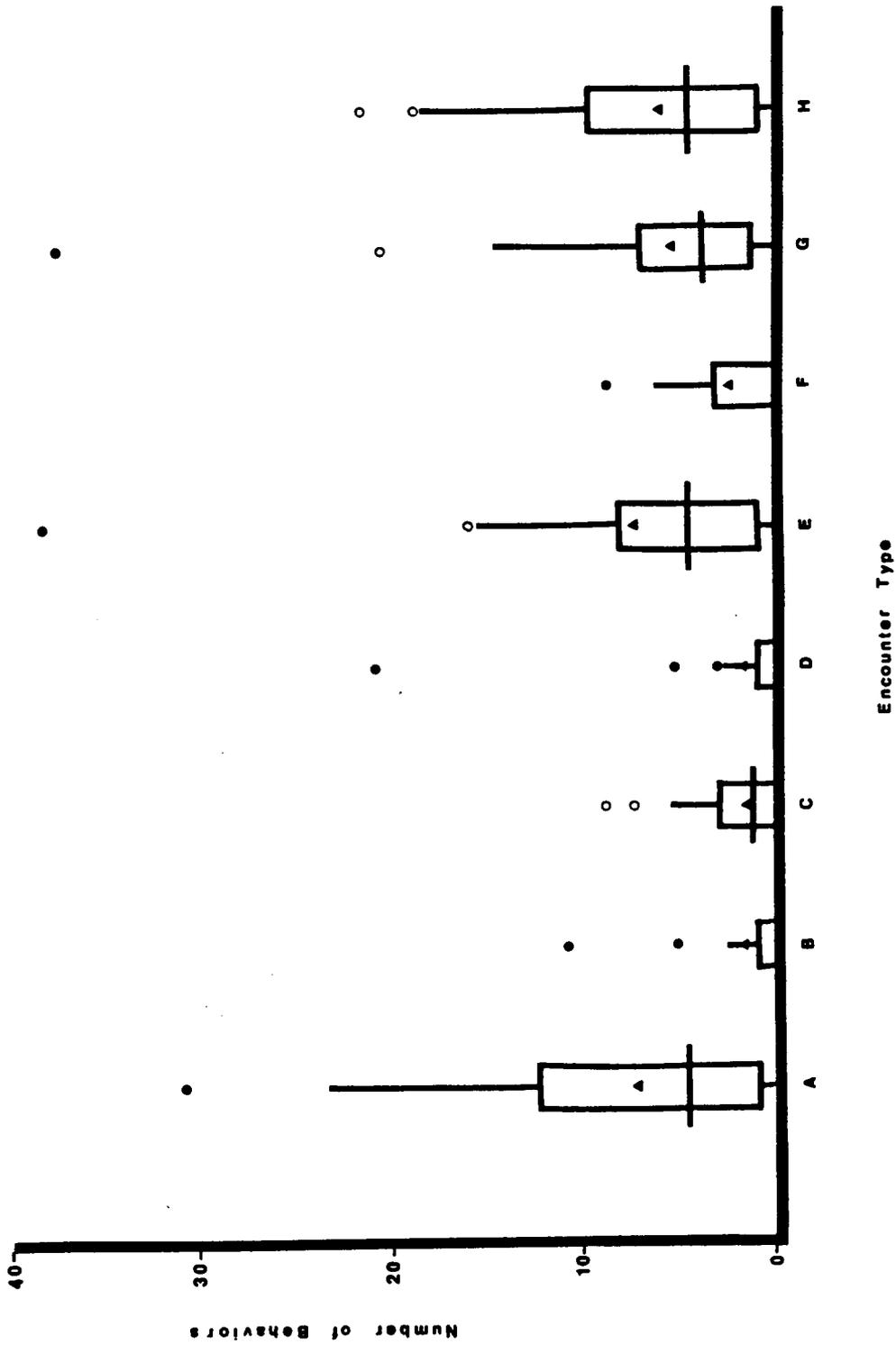


Figure 10. Perineal drag box plots. See Figure 1 for explanation. Box plots lacking a visible median line had a median of zero.

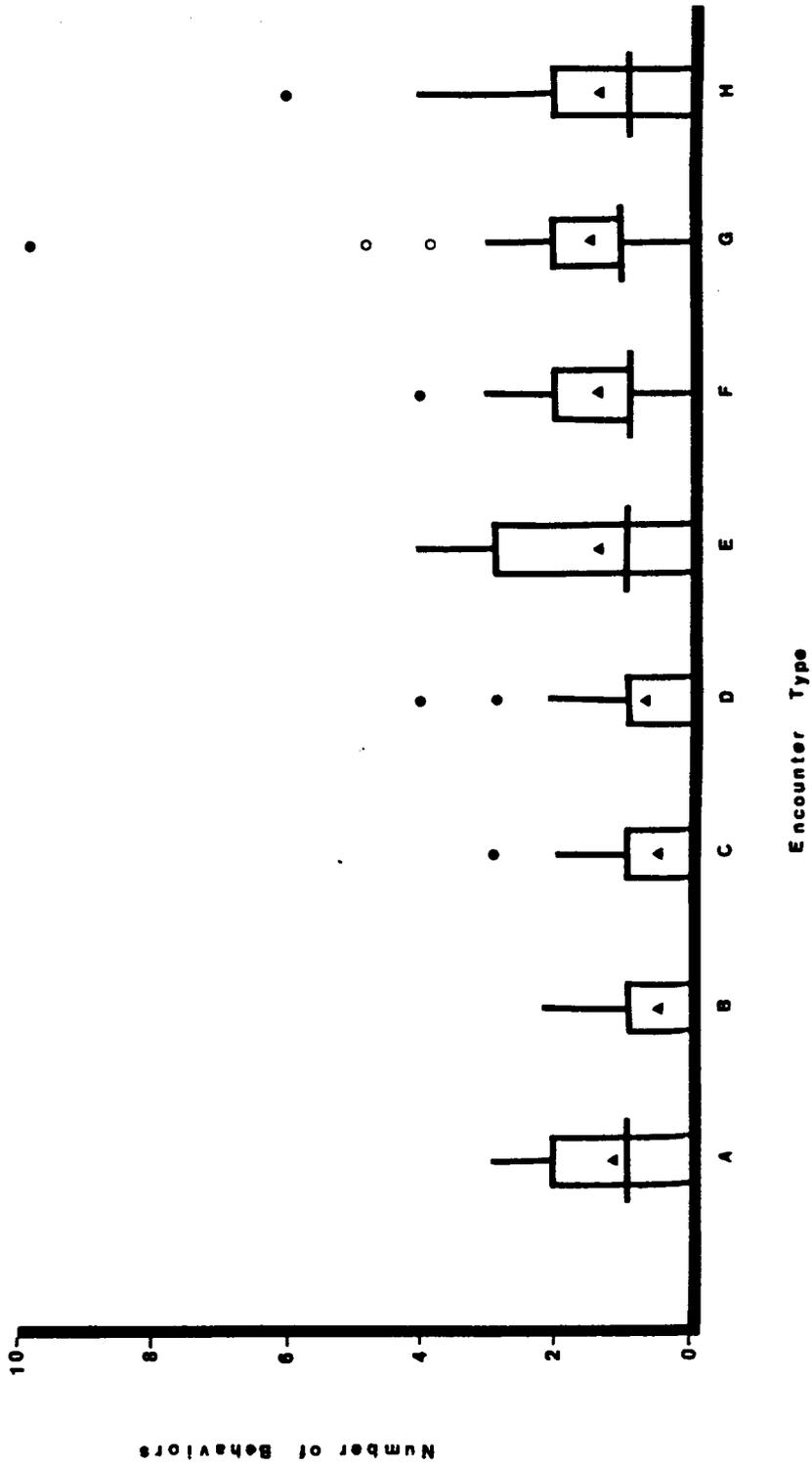


Figure 11. Urine dribble box plots. See Figure 1 for explanation. Box plots lacking a visible median line had a median of zero.

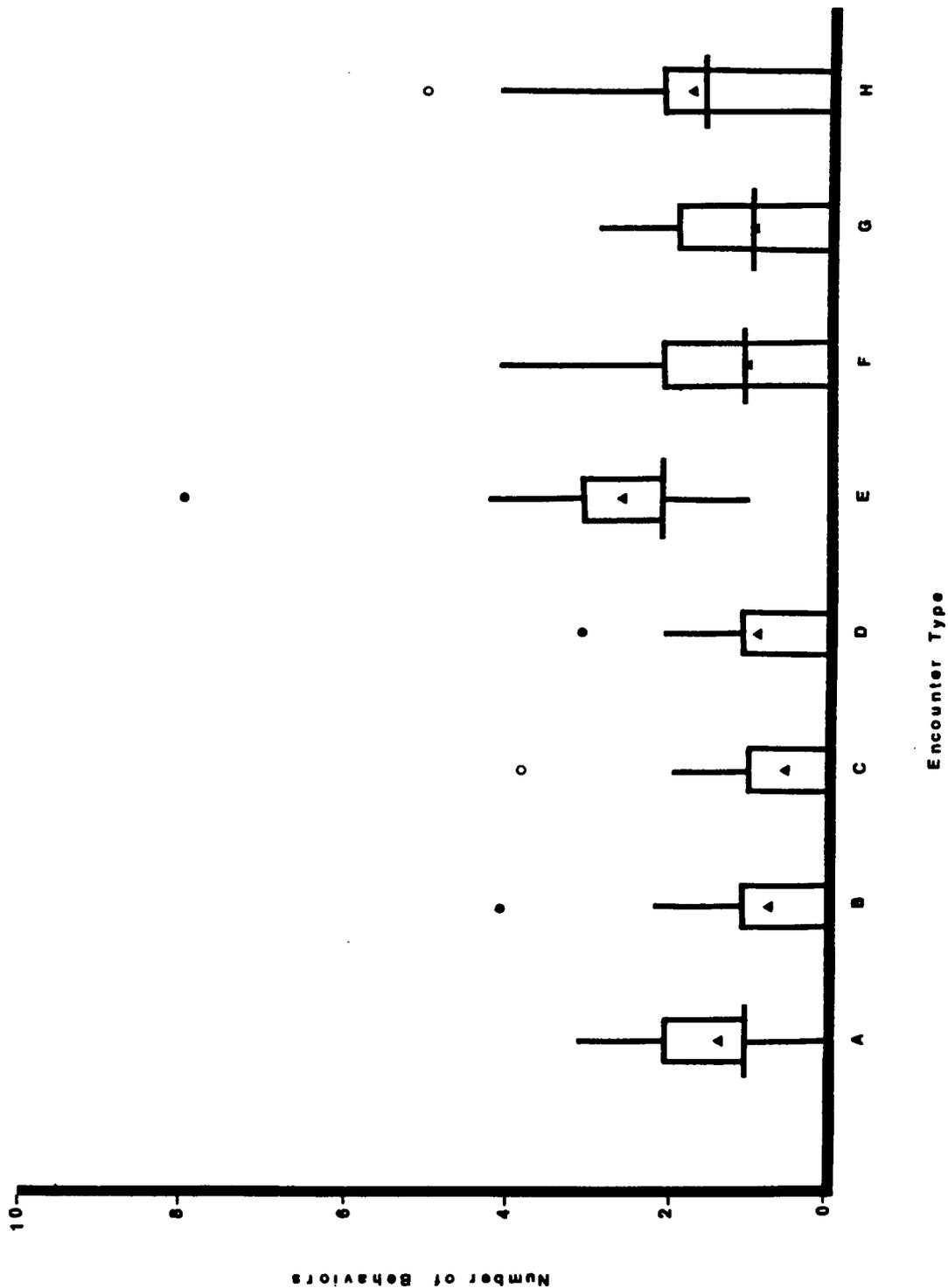


Figure 12. Defecation box plots. See Figure 1 for explanation. Box plots lacking a visible median line had a median of zero.

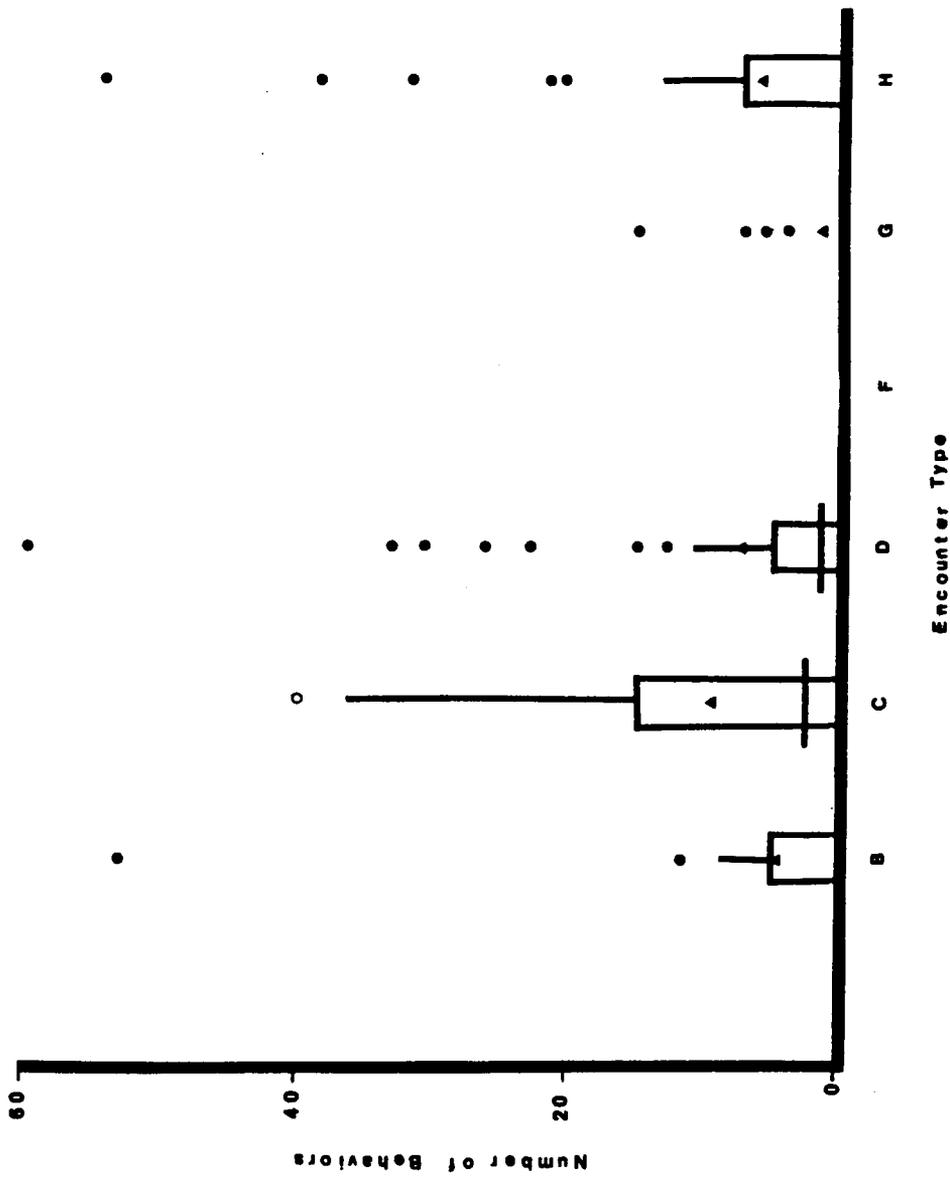


Figure 13. Clicking vocalization box plots. See Figure 3 for explanation. Box plots lacking a visible median line had a median of zero. Box plots were absent and only outliers appeared where most observations had values of zero.

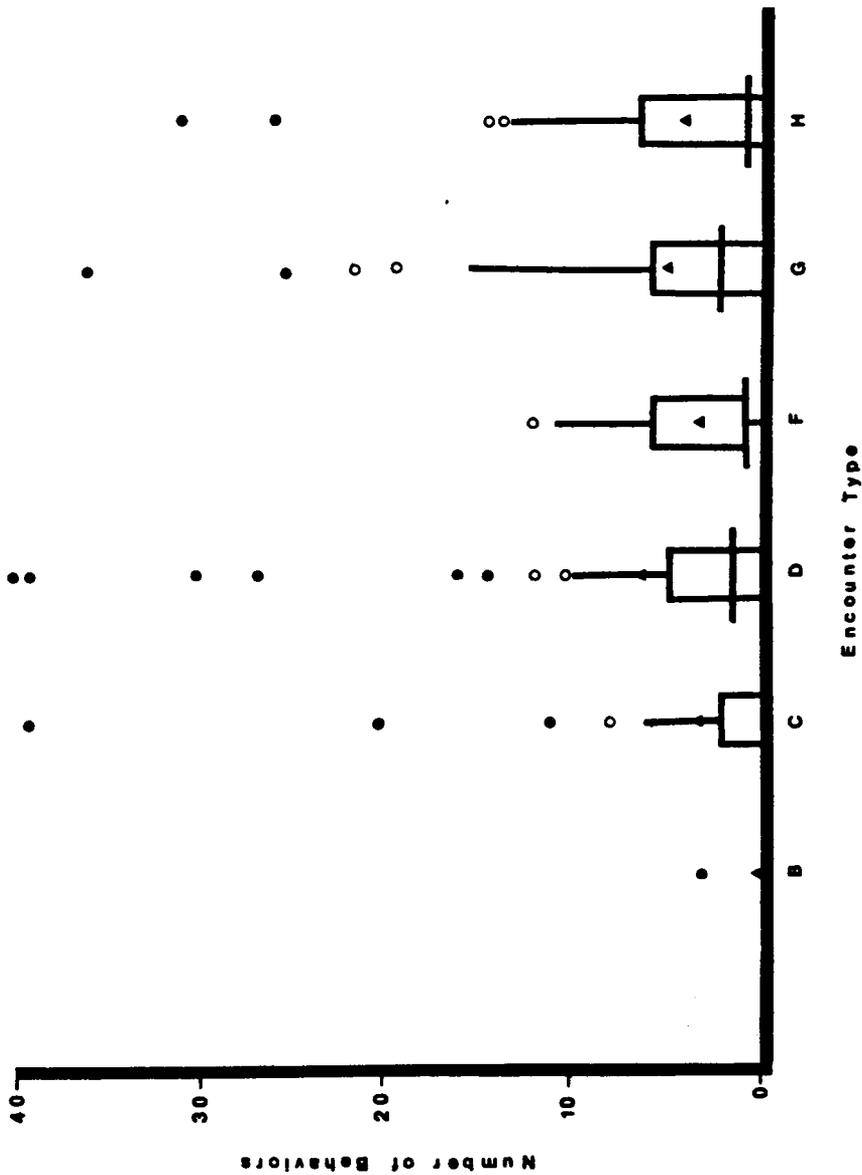


Figure 14. Hiss vocalization box plots. See Figure 3 for explanation. Box plots lacking a visible median line had a median of zero. Box plots were absent and only outliers appeared where most observations had values of zero.

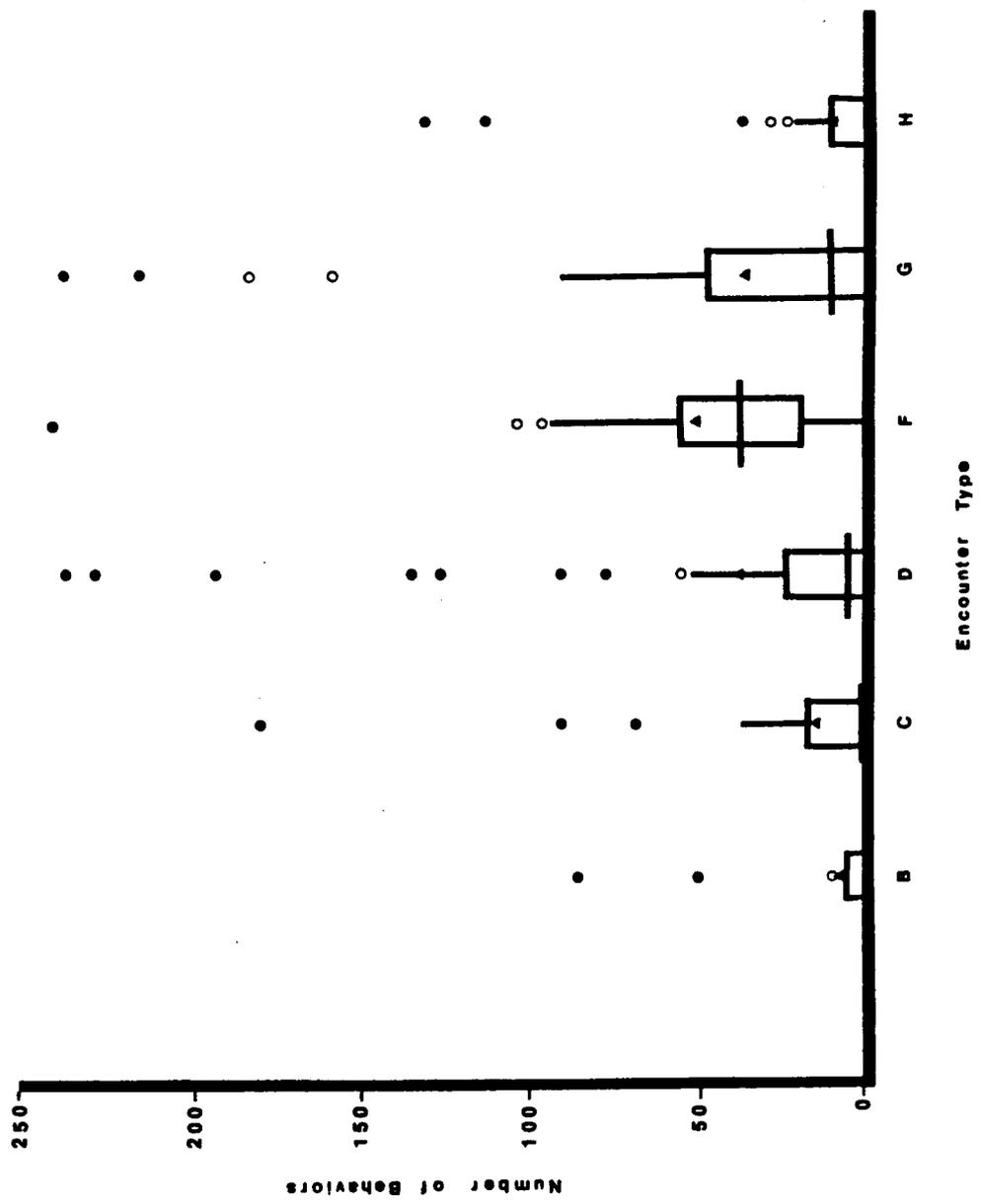


Figure 15. Screech vocalization box plots. See Figure 3 for explanation. Box plots lacking a visible median line had a median of zero.

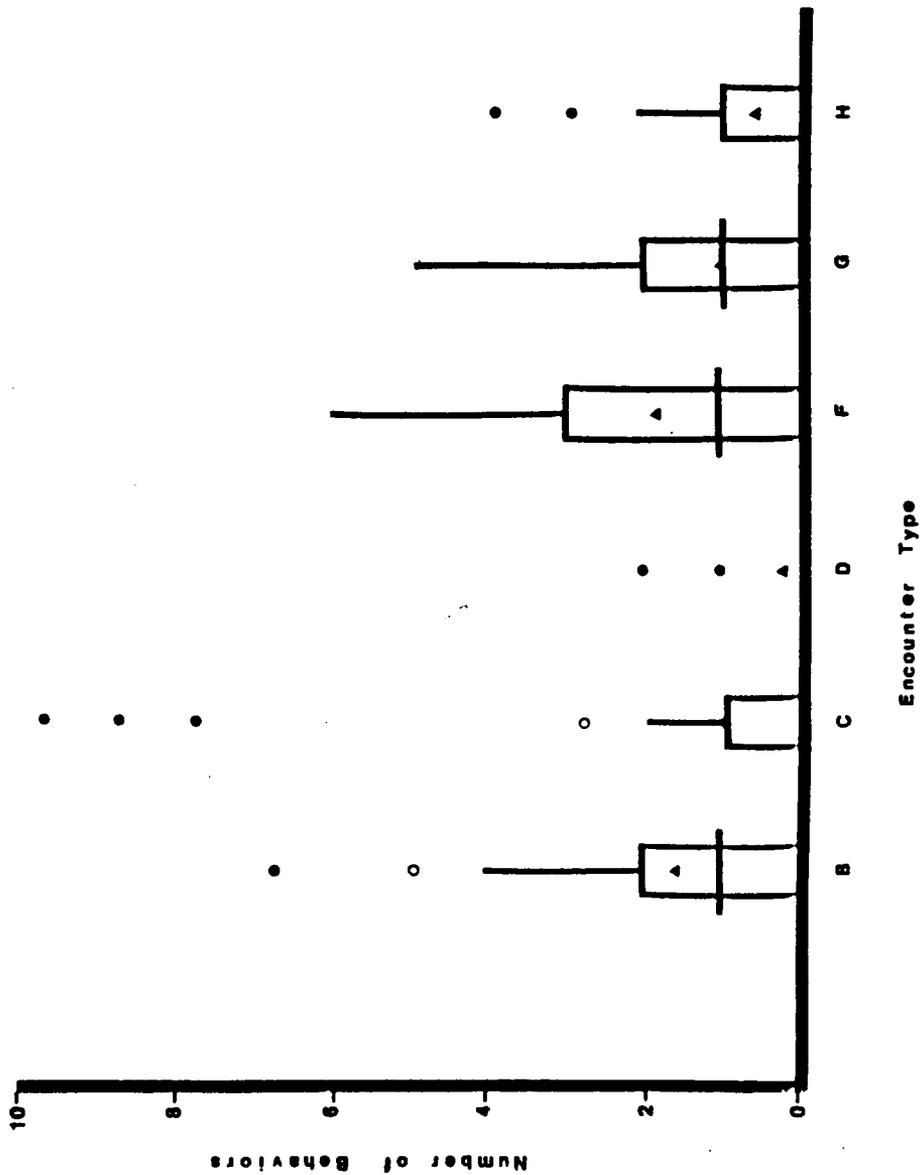


Figure 16. Nose to back contact box plots. See Figure 3 for explanation. Box plots lacking a visible median line had a median of zero.

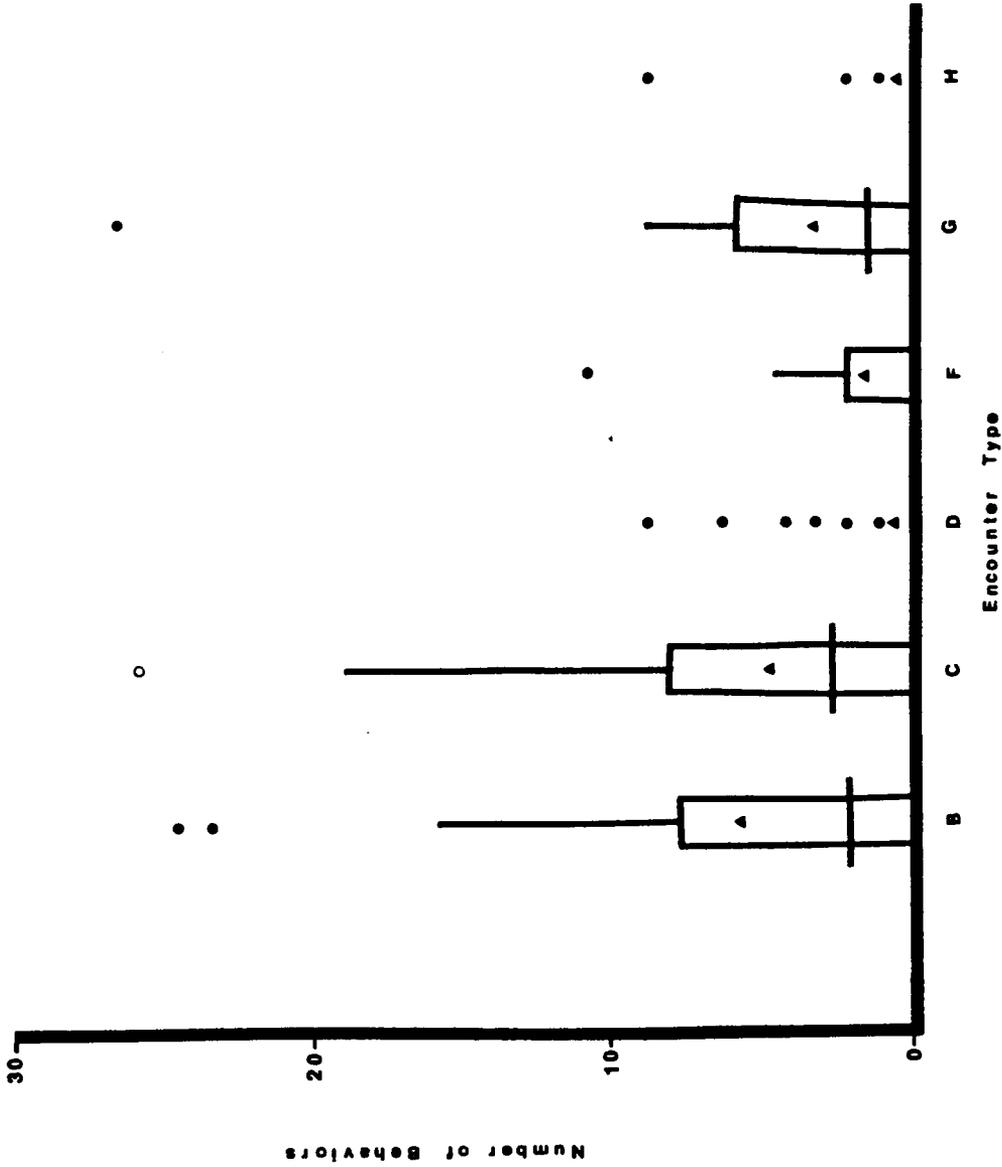


Figure 17. Nose to cloaca contact box plots. See Figure 3 for explanation. Box plots lacking a visible median line had a median of zero. Box plots were absent and only outliers appeared where most observations had values of zero.

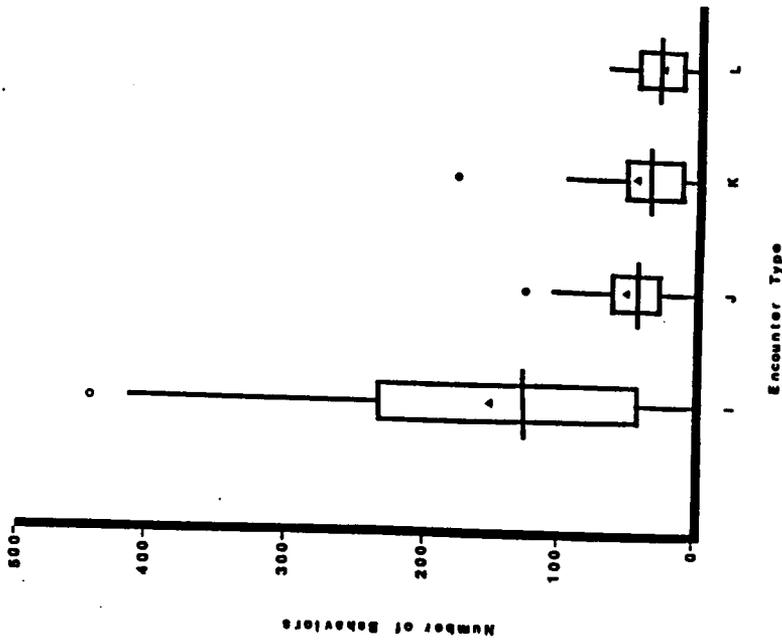


Figure 18. Dominant - subordinate aggressive behavior box plots. From the dyad male-male and female-female encounters I = dominant males (n = 20), J = subordinate males (n = 20), K = dominant females (n = 16), and L = subordinate females (n = 16). The box contains the central 50% of the observations with 25% falling on each side of the median line. Vertical lines extending from the box denote the ranges, open circles denote mild outliers, closed circles denote extreme outliers, and triangles denote means.

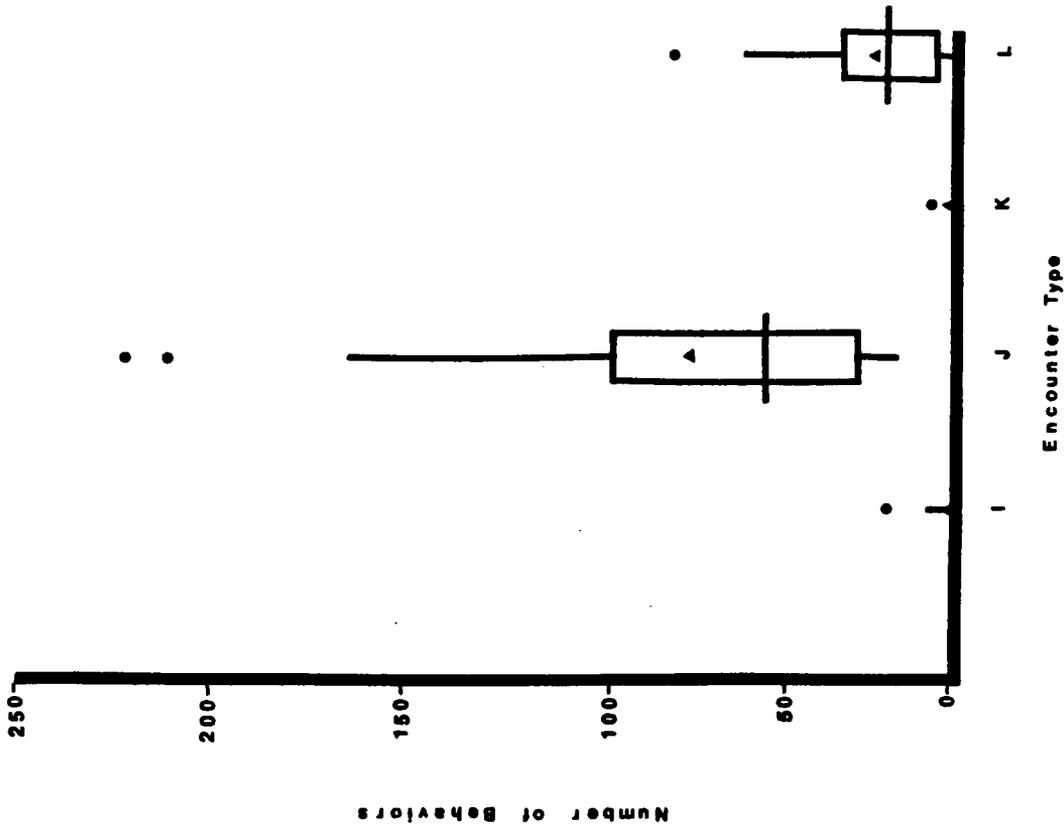


Figure 19. Dominant - subordinate retreating behavior box plots. See Figure 18 for explanation. Box plots were absent and only outliers appeared where most observations had values of zero.

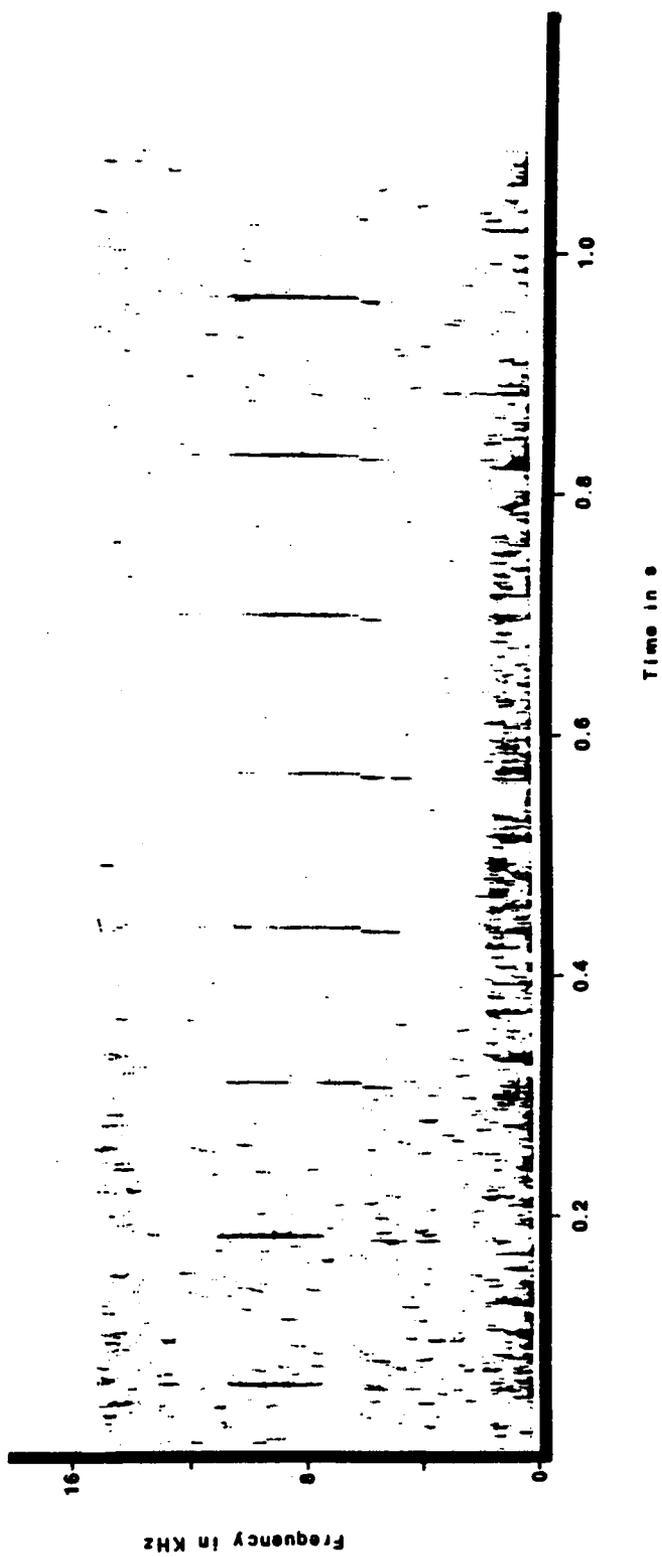


Figure 20. Sonagram of clicking vocalization. Frequency in kHz vs. time in s of a female Monodelphis.

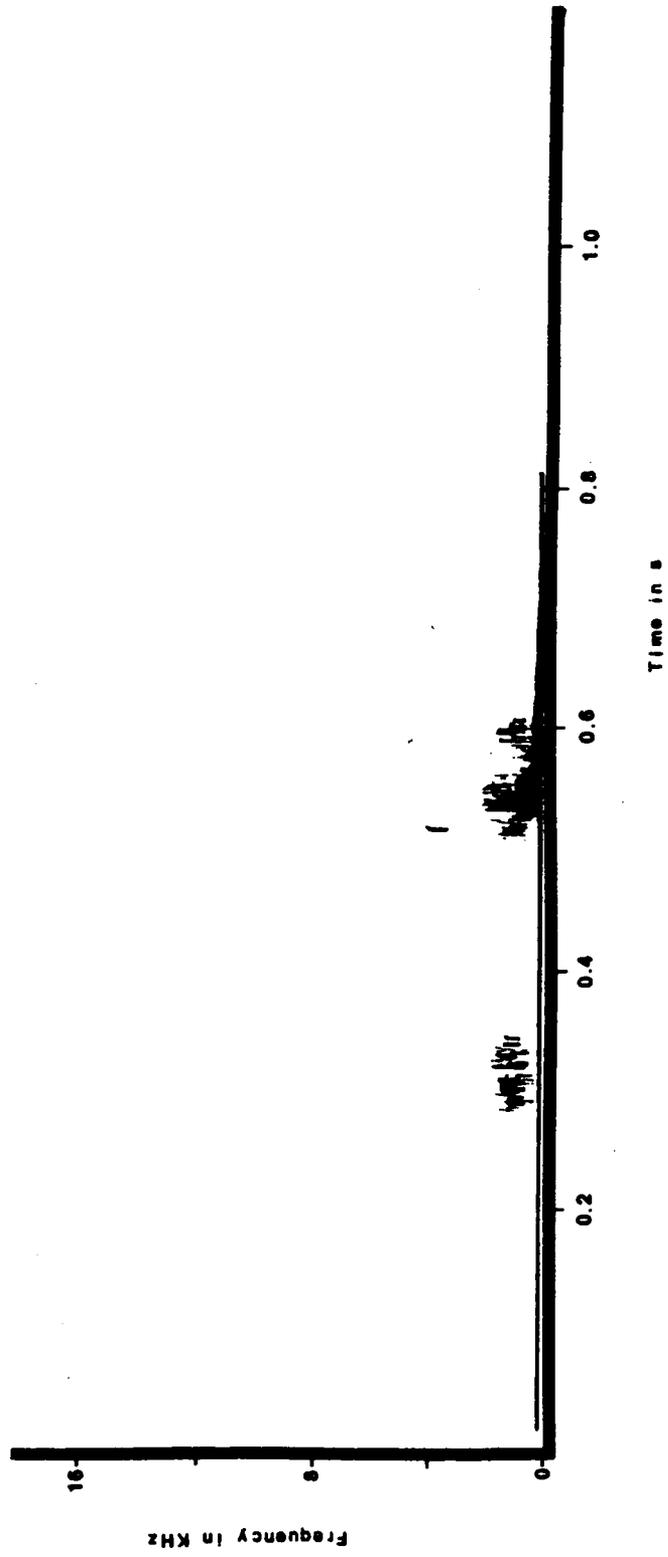


Figure 21. Sonagram of hiss vocalization. Frequency in kHz vs. time in s of a male Monodelphis.

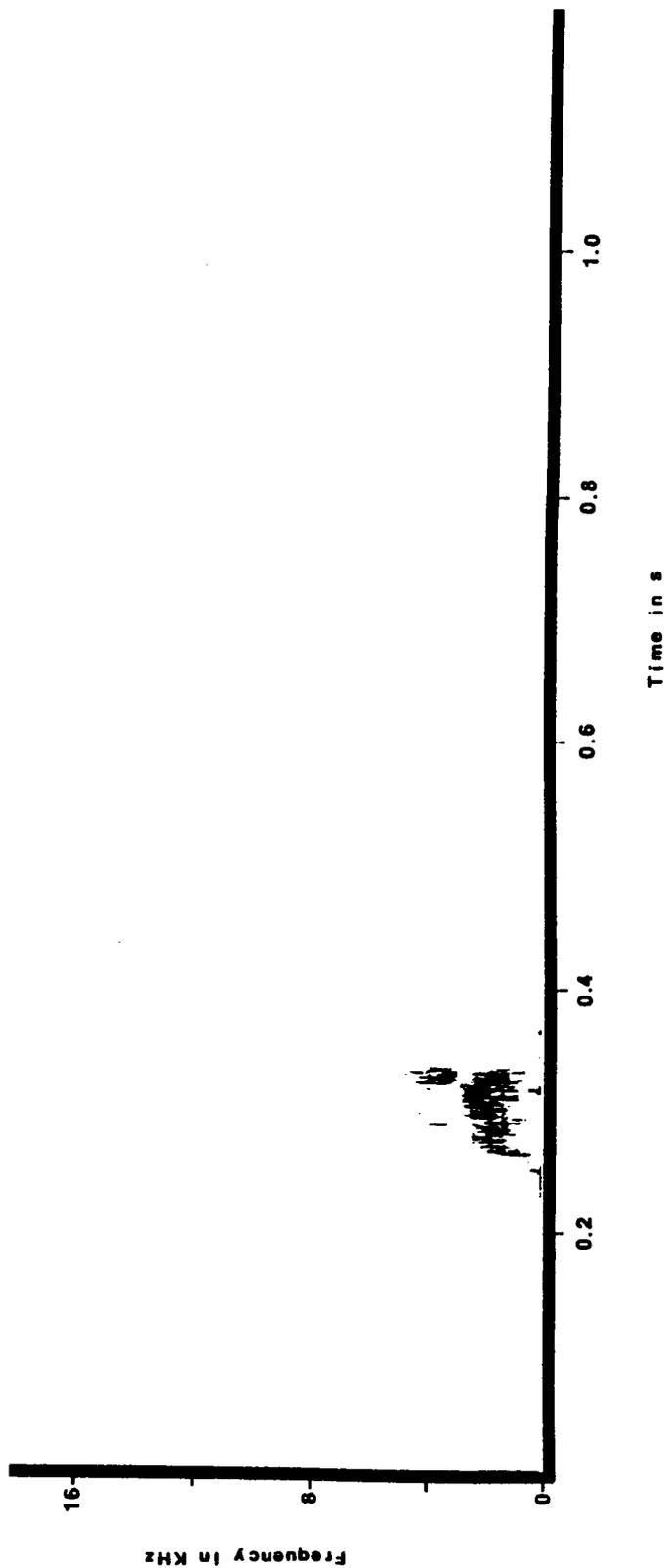


Figure 22. Sonagram of squawk vocalization. Frequency in kHz vs. time in s of a female Monodelphis.

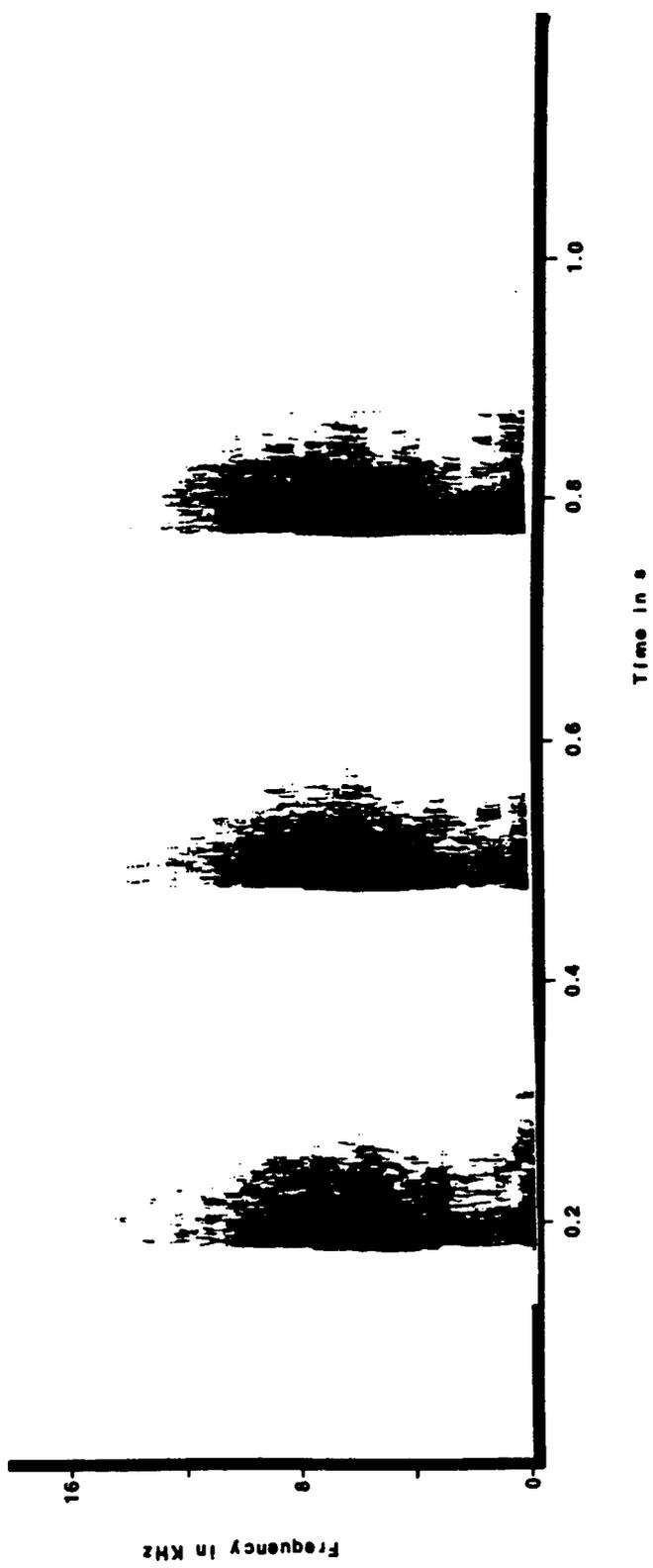


Figure 23. Sonagram of screech vocalization. Frequency in kHz vs. time in s of a female Monodelphis.

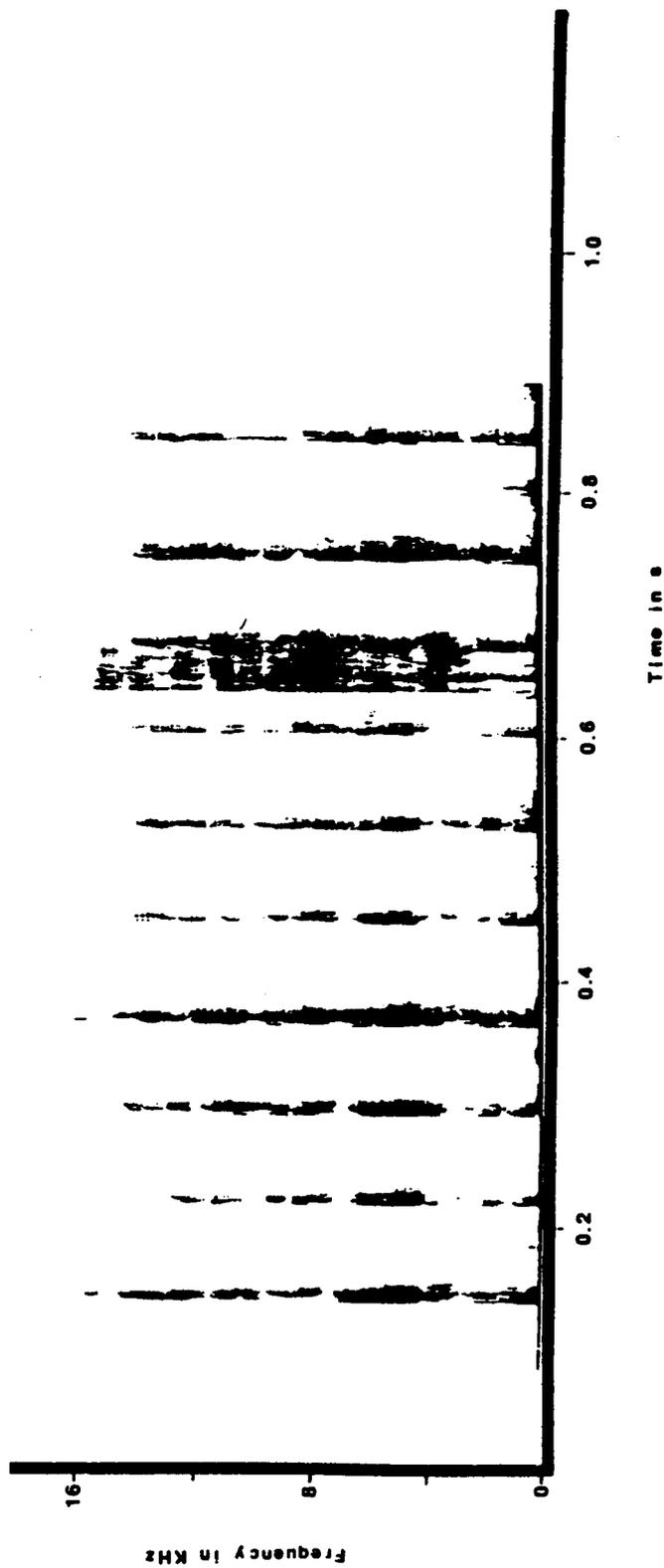


Figure 24. Sonagram of chitter vocalization. Frequency in kHz vs. time in s of a male Monodelphis.

Table 1

Behavioral Catalogue

GROOMING AND RESTING BEHAVIORS

- Hindfoot scratch.....hindfoot body scratching.
- Hindfoot-lick scratch..same as above except foot was licked between scratches.
- Face wash.....grooming facial region and ears with forelegs while sitting on haunches.
- Body groom with mouth..licking and grooming body directly with mouth.
- Genital groom.....grooming genital region with the mouth.
- Scratch.....foreleg body scratching.
- Shake.....shaking the body to remove bark or other debris, often seen after burrowing.
- Allogrooming.....grooming another individual.
- Yawn.....yawning.
- Resting.....sitting on all four legs, eyes open, staring straight ahead.

EXPLORATORY BEHAVIORS

- Dig.....digging in substrate with fore and hind legs.
- Burrow.....burrowing in substrate with head and forelegs.
- Explore.....moving around arena sniffing air or ground but not stopping.
- Sniff.....stops moving, raises head, sniffs the air.
- Sniff the wall.....sniffs at the wall of the arena.
- Sniff the substrate....stops moving about to sniff one spot on the substrate.
- Tongue protrusion.....sticking tongue out into air with head raised.
- Upright sniff.....sniffs air while erect on hind legs balancing with tail.

ATTENTIVE BEHAVIOR

Attentive.....staring at or watching another animal.

SCENT MARKING BEHAVIORS

Perineal drag.....marking by depressing and dragging the perineal region.

Dig perineal drag.....propelling substrate over perineal region by digging.

Metasternal rub.....rubbing the metasternal gland region on an object.

Chin rub.....rubbing the chin region of the body on an object.

Side rub.....rubbing the side of the body postcranially on an object.

Hip rub.....dragging the hip region laterally by pulling the body forward with the forelegs.

Urine dribble.....deposits drops of urine, tail usually moved up and down in the process.

Defecation.....animal deposits feces.

Sniff scent mark.....following any specific scent marking behavior a sniff directed at that mark.

VOCALIZATIONS

Clicking.....tooth chatter like sound produced during courtship and submissive contexts.

Hiss.....low intensity sound in agonistic encounters.

Squawk.....vocalization emitted during fights.

Screech.....high intensity sound in agonistic encounters.

Chitter.....a rapid series of screech-like components.

SOCIAL CONTACT BEHAVIORS

Approach.....approaching a conspecific.

Nose to nose.....sniffing or touching nose of conspecific.

Nose to head.....sniffing or touching head of conspecific.

Nose to neck.....sniffing or touching neck of conspecific.

Nose to back.....sniffing or touching mid-dorsal back of conspecific.

Nose to side.....sniffing or touching side of conspecific from the neck posteriorly.

Nose to abdomen.....sniffing or touching the abdominal region of conspecific.

Nose to rump.....sniffing or touching dorsal posterior end of conspecific.

Nose to cloaca.....sniffing or touching cloaca of conspecific.

Nose to tail.....sniffing or touching tail of conspecific.

Circle.....two animals mutually sniffing each other in the cloacal region, circling in the process.

AGGRESSIVE BEHAVIORS

Follow.....following a conspecific, but not close enough to sniff tail.

Gape.....mouth open with the teeth bared.

Upright threat.....animal sitting on hind legs gaping.

Paw threat.....sitting on haunches swinging forelegs at opponent.

Chase.....chase opponent, both running.

Lunge.....jump at opponent.

Bite.....biting opponent.

Bite and shake.....biting another individual and then shaking it with its teeth.

Fight.....a fight with the two animals frequently locked together.

Ears forward.....ears projected in a forward direction.

Tail down.....tail held low to ground and often dragged.

RETREAT BEHAVIORS

- Jump back.....leap away from opponent.
- Retreat.....run away a short distance from opponent.
- Run in circles.....retreating such that the animal runs in a circle around perimeter of arena.
- Ears back.....ears held back to sides or down.
- Tail up.....tail carried off ground pointing upward beyond the horizontal.

SEXUAL BEHAVIORS

- Grasp.....grasping or grabbing conspecific with forelegs.
- Neck grip.....male biting dorsal nape of female's neck.
- Mount.....male mounts female.

OTHER BEHAVIORS

- Run.....animal runs around enclosure.
- Leave.....animal walks away from conspecific.
- Jump.....animal tries to jump up sides of arena.
- Nip substrate.....animal chews at substrate.

Table 2. Statistical probabilities for behaviors in neutral test encounters. All comparisons used the Median test except BxF and CxG, which used the Sign test. A = solitary males, B = familiar males (of the familiar male-female pairings), C = unfamiliar males (of the unfamiliar male-female pairings), D = dyad males (of the male-male pairings), E = solitary females, F = familiar females (of the familiar male-female pairings), G = unfamiliar females (of the unfamiliar male-female pairings), H = dyad females (of the female-female pairings). * = .01 < p < .05, ** = .001 < p < .0009, and *** = .0001 < p < .00009. Letters adjacent to p-values indicate which individual type was significantly higher. A (--) = non-significant. A (-) indicates where statistical comparisons were not performed because an overall within sex Median test was not significant or the behavior did not occur in that encounter type.

Encounter Comparison	Context		Scent			
	Grooming and Resting	Exploratory	Attentive	Marking	Vocalizations	Aggressive
AxB	** A	*** A	--	* A	-	-
AxC	*** A	*** A	--	--	-	-
AxD	* A	*** A	--	* A	-	-
BxC	** B	* B	--	** C	** C	--
BxD	--	--	*** D	--	* D	*** D
CxD	* D	--	** D	** C	--	*** D
ExF	*** E	*** E	--	--	-	-
ExG	*** E	*** E	--	--	-	-
ExH	* E	*** E	--	--	-	-
FxG	--	* F	* G	--	* F	* G
FxH	** H	*** H	** H	--	*** F	--
GxH	*** H	*** H	*** H	--	--	** G
BxF	** F	--	--	--	* F	--
CxG	** G	--	--	--	--	** G
DxH	*** H	*** H	--	* H	--	*** D

Table 3. Statistical probabilities for scent marking modes. Statistical tests, encounter contexts, and symbols are as in Table 2.

Encounter Context Comparison	Perineal		Dig Perineal		Chin		Hip		Urine		Defecation
	Drag		Drag		Rub		Rub		Dribble		
AxB	**	A	-	-	-	-	-	-	-	-	* A
AxC	**	A	-	-	-	-	-	-	-	-	** A
AxD	**	A	-	-	-	-	-	-	-	-	* A
ExF	-		-	-	-	-	-	-	-	-	** E
ExG	-		-	-	-	-	* G	-	-	-	** E
ExH	-		-	-	-	-	-	-	-	-	--
FxH	-		-	-	-	-	-	-	-	-	--
GxH	-		-	-	-	-	-	-	-	-	--
BxF	--		--	G	--		--	G	**	F	--
CxG	**	G	**	G	* C		**	G	**	G	* G
DxH	***	H	--		--		**	H	--		* H

Table 4. Statistical probabilities for vocalizations. All comparisons used the Median test except BxF and CxG, which used the Sign test. B = familiar males (of the familiar male-female pairings), C = unfamiliar males (of the unfamiliar male-female pairings), D = dyad males (of the male-male pairings), F = familiar females (of the familiar male-female pairings), G = unfamiliar females (of the unfamiliar male-female pairings), H = dyad females (of the female-female pairings). * = .01 < p < .09, ** = .001 < p < .009, *** = .0001 < p < .0009. Letters adjacent to p-values indicate which individual type was significantly higher. A (--) = non-significant. A (-) indicates where statistical comparisons were not performed because an overall within sex Median test was not significant or the behavior did not occur in that encounter type.

Encounter Context	Comparison	Clicking	Hiss	Squawk	Screech	Chitter
BxC	-	-	* C	--	--	-
BxD	-	-	*** D	--	--	-
CxD	-	-	* D	* D	* D	-
FxC	--	--	-	-	* F	* F
FxH	** H	-	-	-	*** F	* F
GxH	** H	-	-	-	** G	--
BxF	--	-	** F	--	** F	* F
CxG	** C	-	--	--	* G	--
DxH	--	-	--	--	* D	-

Table 5. Statistical probabilities for social contact behaviors. Statistical tests, encounter contexts, and symbols are as in Table 4.

Encounter Context Comparison	Nose to Back	Nose to Side	Nose to Cloaca
BxD	* B	* B	*** B
CxD	* C	* C	*** C
FxH	* F	-	--
GxH	* G	-	*** G
BxF	--	--	* B
CxG	--	* G	* C

Table 6. Statistical probabilities for dominant - subordinant context comparison in dyad encounters. The Median test was used for IxK and JxL, the Sign test was used for IxJ and KxL. I = dominant males, J = subordinant males, K = dominant females, and L = subordinant females. * = $.01 < p < .05$, ** = $.001 < p < .009$, and *** = $.0001 < p < .0009$. Letters adjacent to p-values indicate which individual type was significantly higher. A (--) = non-significant.

Encounter Context Comparison	Grooming and Resting	Exploratory	Attentive	Scent Marking	Vocalizations	Social Contact	Aggressive	Retreat
IxJ	--	--	--	--	* J	** I	** I	** J
KxL	--	--	** L	* K	--	** K	--	** L
IxK	*** K	** K	--	* K	--	--	** I	--
JxL	** L	*** L	--	--	--	--	--	* J

Table 7. Statistical probabilities for dominant - subordinate context comparisons in dyad encounters for A. scent marking modes, B. vocalizations, and C. social contact. Statistical tests, encounter contexts, and symbols are as in Table 6.

A. Encounter Context Comparison		Perineal Drag	Chin Rub	Hip Rub	Defecation
IxJ		--	* I	--	* J
KxL		* K	--	* K	* K
IxK		*** K	--	** K	** K

B. Encounter Context Comparison		Clicking	Screech
IxJ		* J	** J

C. Encounter Context Comparison		Approach	Nose to Nose	Nose to Rump
IxJ		** I	--	* I
KxL		** K	* K	--

Table 8. Sonographic vocalization analysis. Sample sizes were *n = number of animals, **n = number of vocalizations in which variable could be measured, ***n = number of intervals between vocalizations. Chitter components are also presented since chitters are rapid series of "screech-like" sounds. Maximum frequencies for screeches and chitters (\$) could not be determined due to equipment limitations.

Vocalization (*n)	Syllable Type	Duration (**n) mean ± S.D. (msec)	Interval (***) mean ± S.D. (msec)	Mean minimum and (**n) Maximum frequency of Audible Vocalizations (kHz)
Click (Males) (3) (Females) (3)	III	3.41 ± 2.13 (45)	140.9 ± 20 (34)	4.4 - 13.6 (13)
Hiss (Males) (3) (Females) (5)	IV	253.7 ± 189 (24)	129.0 ± 5.9 (31)	5.0 - 11.4 (32)
Squawk (Males) (6) (Females) (6)	IV	155.3 ± 78 (30)	762.5 ± 114 (4)	0.5 - 4.4 (22)
Screech (Males) (4) (Females) (11)	II	160.5 ± 125 (22)	192.9 ± 155 (9)	0 - 3.3 (30)
Chitter (Males) (4) (Females) (3)	II	138.1 ± 106 (9)	non-repeated non-repeated	0 - 3.2 (21)
Chitter (Males) (4) (Females) (3)	II	80.4 ± 25 (23)	156.9 ± 65 (14)	0.3 - 3.8 (9)
Chitter (Males) (4) (Females) (3)	II	657.84 ± 232.51 (11)	224.8 ± 140 (47)	1.3 - \$ (23)
Chitter (Males) (4) (Females) (3)	II	75.1 ± 27.8 (86)	non-repeated non-repeated	1.9 - \$ (58)
Chitter (Males) (4) (Females) (3)	II	481.08 ± 158.28 (5)	52.6 ± 30 (82)	0 - \$ (11)
Chitter (Males) (4) (Females) (3)	II	29.6 ± 19 (89)	46.8 ± 27 (18)	0.5 - \$ (5)
Chitter (Males) (4) (Females) (3)	II	35.6 ± 26 (23)		0.5 - \$ (5)

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