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Source: *Journal of Mammalogy*, Vol. 72, No. 2 (May, 1991), pp. 402-410
Published by: American Society of Mammalogists
Stable URL: https://www.jstor.org/stable/1382114
Accessed: 06-01-2023 20:47 UTC

SOCIAL BEHAVIOR IN CAPTIVE VIRGINIA OPOSSUMS, *DIDELPHIS VIRGINIANA*

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Abstract.—To examine social behavior in Virginia opossums (*Didelphis virginiana*) systematically, spontaneous interactions and nesting behavior of three mixed-sex groups of adults were observed in a seminatural setting during a 7-month period including segments of breeding and nonbreeding seasons. Interactions were predominantly affiliative or nonagonistic, and nesting associations also indicated a greater capacity for social tolerance than generally is recognized for didelphid marsupials. The overall frequency of social interactions peaked with onset of breeding in January, and intrasexual agonistic encounters (primarily female-female) occurred more often than male-female encounters. Opossums readily formed stable linear-dominance hierarchies, with females usually dominant. These data suggest that opossum sociality is better developed than generally recognized, and that seasonal influences should be considered when assessing social complexity in this species.

The New World metatherian family Didelphidae consists of ca. 75 species, most of which inhabit tropical and subtropical habitats (Hunsaker, 1977; Marshall, 1982). Because it is the oldest extant mammalian family (Clemens, 1968), and its members in general are morphologically conservative, nocturnal, ecological generalists, many authors have suggested that didelphid sociality should provide an indication of the social patterns of early mammals (Charles-Dominique, 1983; Eisenberg, 1980, 1981; Russell, 1985). Although few behavioral data exist for didelphids, sociality in this group frequently is dismissed as primitive relative to that of other mammalian families (Charles-Dominique, 1983; Hunsaker and Shupe, 1977).

Didelphis virginiana, the Virginia opossum, is nocturnal and largely solitary, with a diffuse system of overlapping home ranges (Gardner, 1982; Gillette, 1980; Ryser, 1990; Sunquist et al., 1987). Radiotracking data suggest that its mating system is promiscuous or polygynous (Austad, 1984; Eisenberg, 1988; Ryser, 1990; Sunquist et al., 1987). Females are seasonally polyestrous, and breed in the northern United States from mid-January to late July or August. Opossums reach sexual maturity at approximately 8 months of age, but do not breed until the first estrus the following year (Gardner, 1982; Reynolds, 1952). Wild opossums surviving to breeding age live an average of 17 months (M. Sunquist, pers. comm.), hence yearling females comprise most of the breeding population.

Published observations of social patterns have been descriptive, rather than quantitative (McManus, 1967, 1970; Reynolds, 1953), except those of Hayssen (1985), and usually have involved staged encounters between captive animals of unspecified age and breeding status. Sociality in *Didelphis* has been consistently dismissed as "simple," "poorly developed," or characterized almost exclusively by aggression or avoidance (Charles-Dominique, 1983; Gardner, 1982; McManus, 1970, 1974; Reynolds, 1953). Despite reports of opossums sharing or alternately using dens in nature (Fitch and Shirer, 1970; Lay, 1942; Pippitt, 1976; Reynolds, 1945; Ryser, 1990; Yeager, 1936), no capacity for affiliative interactions has been reported for adults in either the resting or the active period. Available data are equivocal regarding the ability of opossums to form even elementary social relationships, such as dominance hierarchies, or to respond to conspecifics in any stable, predictable way based on individual recognition or the outcome of previous encounters.

To test the hypothesis that opossum social behavior is predominantly agonistic, the general frequency and composition of spontaneous interactions, including nesting associations, was examined in small groups of *D. virginiana* of known age in seminatural enclosures. Because few affiliative interactions are documented, I focussed particularly on the relative frequencies of agonistic, nonagonistic, and sexual encounters. The capacity of opossums to maintain stable, organized social patterns in the form of linear dominance hierarchies also was studied. To assess the impact of the onset of breeding on frequencies of social interactions of different types, observations were conducted during a 7-month period including segments of both breeding and nonbreeding seasons.

METHODS

The 15 adult opossums studied were born in January or February of the 1983 breeding season to females live trapped in northwestern Ohio. At 100–115 days of age (approximate age of juvenile dispersal), littermates were separated and placed in small groups of unrelated individuals. At sexual maturity (7–8 months of age), they were placed in new groups (three females and two males each) of unrelated animals with which they had no previous social or sexual experience. This type of group composition was intended to simulate as closely as possible the natural situation, in which subadult opossums may disperse from their natal home ranges, and certainly encounter individuals less closely related than siblings. All animals were marked with numbered fluorescent ear tags for individual recognition.

Each group was housed in an indoor dog kennel (3.7 by 3.7 by 2.4 m) connected to an adjoining outdoor run to which animals were permitted access except during observations or when the temperature outdoors was below freezing. Indoor temperature was allowed to vary freely ($\bar{X} \pm SE$, 13.6 ± 1.62°C), but not to fall below freezing, and natural light was admitted by large windows at ceiling level. Kennels had concrete floors covered with a layer of wood shavings and a network of wooden perches; wooden nestboxes (30.5 by 30.5 by 45.8 cm) and bedding were provided for each animal.

Diet consisted of 50 g of high-protein dry cat food per animal daily plus supplements of fruit, eggs, liver, and vitamins. Animals were fed ≥2 h before observations and fresh water was provided ad lib. They were treated for parasites and weighed monthly; any individual that became ill or seriously wounded was removed from its group and treated.

The reproductive status of each female was monitored from 2 weeks before the expected onset of estrus in January until the end of the study. Cells of the reproductive tract were collected by lavage of the urogenital sinus with a medicine dropper; they were then smeared on a glass slide, air dried, stained lightly with methylene blue, and examined under a light microscope. Reproductive status was determined from these smears based on relative numbers of cornified epithelial cells according to published procedure for this species (Fleming and Harder, 1981*a*, 1981*b*; Jurgelski and Porter, 1974). To eliminate a possible source of observer bias, smears taken on the day of a scheduled nocturnal observation session were not examined until several days after that session. Manual inspection of pouches was used to determine birth dates of young to within 2 days. Breeding began the 2nd week in January, as judged from the presence of proestrous and estrous smears, copulatory attempts by males, and extrapolation backward from the dates pouch young appeared (Reynolds, 1952). By mid-January, eight of nine females had been in estrus. "Nonbreeding season" hereafter will refer to the part of the study from October 1983 to 7 January 1984; "breeding season" will refer to the period from the first estrus (8 January) through early April, when observations were terminated.

Two-hundred-eighty-eight 12- to 15-min nocturnal observation periods (58 h total) were conducted between October 1983 and April 1984. These were divided approximately equally among the three groups, and the order in which the groups were observed during a nightly session was randomized. Observations were conducted under red light between 2100 h Eastern Standard Time and midnight from a seat outside the window of each kennel; behavioral data were recorded on cassette tapes and later coded for analysis. Regular hourly surveys of the total number of animals active (all three groups combined) during the first 2 months of the study confirmed they were being observed during their most active period. Nightly activity patterns corresponded in general to those described previously for this species (McManus, 1971; Ryser, 1990), with peak activity occurring around midnight. To examine the relationship between frequency of social interactions and general activity, the number of animals active (engaged in behaviors other than resting or perching) in a group also was recorded for each period. Observations of a group continued until membership fell below three (a male in group 1 was removed in December because of illness; otherwise group composition remained stable until the end of the study in April).

Occupancy of nestboxes in daytime was examined several times a week. If an animal was removed from a group, a nestbox also was removed to keep the number of boxes relative to the number of animals constant during the study.

A social interaction was recorded if an animal approached within 1 m of another; when more than two individuals interacted simultaneously, separate interactions were tabulated for each dyad. Because the main focus was on overall composition and seasonal changes in relative frequencies of different types of interactions, rather than on specific behavior patterns, each interaction was placed in one of three mutually exclusive categories, based on behavioral inventories for this species published elsewhere (Hayssen, 1985; McManus, 1967; Reynolds, 1952). Agonistic interactions involved aggressive or submissive elements performed by one or both members of a dyad, and included threats, fights, chases, and supplants. Sexual interactions included only those involving courtship by males (e.g., rubbing the head or neck on a female, pinning, or mounting), or receptive behavior by females. Neutral or affiliative encounters (tabulated as a single category) consisted of those lacking agonistic elements (including any evidence of avoidance), courtship by males, or receptive behaviors by females. Individual behavior patterns involved included investigative behaviors directed toward other individuals, side-to-side body contact, and feeding or resting <1 m apart for periods longer than several seconds.

Dominance matrices were constructed for each group based on the outcome of agonistic encounters (fights or supplants) with clear winners according to convention (Bernstein, 1970, 1981; Chase, 1974; Rowell, 1974; Fig. 1). An individual was judged dominant over others against which it had accrued more wins than losses. If two animals won encounters with the same number of individuals, the one with more wins overall was considered dominant; individuals distinguished by neither of these criteria were given tied ranks. The resulting matrices were arranged with dominant individuals at the top and subordinates on the bottom, and the highest ranking animal given a rank of one.

The direction inconsistency index (de Waal, 1977; Schilder, 1988) was calculated for each dominance matrix to determine the degree of unidirectionality of agonistic interactions (Fig. 1). Additionally, the Landau (1951) test was performed on each matrix to obtain h, a measure of the linearity of a dominance relationship. Because probability levels for Landau scores are not available for groups of five or fewer animals (Appleby, 1984), this index was used only as an indicator of the applicability of a rank-order model to agonistic relationships, and was not interpreted inferentially.

Descriptive statistics, and regression and correlation analyses were generated by use of SAS (SAS Institute, Inc., 1985) or SYSTAT (Wilkinson, 1988). All tests for significance of Spearman rank correlation coefficients (r_s) were two-tailed. Zar (1984) was consulted for χ^2 contingency analyses.

RESULTS

Of 2,194 spontaneous social interactions recorded in the study, 1,168 (53%) were neutral or affiliative and 856 (39%) were agonistic. Seventeen (<1%) were sexual; the remaining 7% could not be classified because of difficulty observing them in their entirety. Male-female interactions accounted for 1,349 (62%) of the 2,170 interactions for which the sex of the participants was noted. Female-female interactions comprised 627 (29%). Only 9% of encounters were between males. When agonistic interactions were analyzed separately, intersexual encounters were as frequent as intrasexual interactions.

The degree of affiliation seen in neutral or affiliative interactions ranged from indifference to sustained and apparently deliberate physical contact or proximity. Of 510 interactions in this category for which individual behavioral elements were recorded, approximately one-half involved an approach of one animal to ≤ 1 m of another and elicited little or no response on the part of the recipient. Forty-five percent (229) involved investigation of one participant by another (e.g., nose to nose contact, anogenital sniffing). Six percent (33) involved animals feeding or resting out of a nestbox no more than a few centimeters apart. A small proportion (2%), involved slowly brushing bodies side to side as one animal walked past another. Licking of one individual by another was seen only twice; there was no evidence of mutual grooming.

Neutral or affiliative interactions were distributed nonrandomly among dyads in all three groups (tests of goodness of fit to a random distribution of interactions among dyads resulted in χ^2s with $P < 0.001$ for all three groups). The proportion of interactions of this type contributed by a given dyad ranged from 3 to 26%. Male-female dyads did not account consistently for the highest percentages of interactions contributed, nor did the male-male dyad in each group always account for the lowest percentage.

There was considerable variability in both frequency of social interactions and levels of general

Group 1

NONBREEDING SEASON

Winners	Losers					Totals	Rank
	7♀	19♂	8♀	4♀	17♂		
7♀		1	1	1	1	4	1
19♂	0		2	2	5	9	2
8♀	0	0		5	1	6	3
4♀	0	1	0		2	3	4
17♂	0	0	0	0		0	5

D.I.: 0.05 Grand Total: 22
h: 1.00

BREEDING SEASON

Winners	Losers				Totals	Rank
	7♀	4♀	19♂	8♀		
7♀		19	11	0	30	1
4♀	1		6	2	9	2
19♂	0	2		0	2	3
8♀	0	2	2		4	4

D.I.: 0.12 Grand Total: 45
h: 1.00

Group 2

NONBREEDING SEASON

Winners	Losers					Totals	Rank
	9♀	2♀	30♂	5♀	20♂		
9♀		12	3	10	18	43	1
2♀	0		2	1	2	5	2
30♂	2	1		1	1	5	3
5♀	1	0	2		1	4	4
20♂	0	2	6	0		8	5

D.I.: 0.22 Grand Total: 65
h: 0.90

BREEDING SEASON

Winners	Losers					Totals	Rank
	9♀	20♂	5♀	30♂	2♀		
9♀		46	21	19	61	147	1
20♂	2		0	27	8	37	2
5♀	2	2		2	1	7	3
30♂	2	0	1		1	4	4
2♀	0	3	0	0		3	5

D.I.: 0.06 Grand Total: 198
h: 1.00

Group 3

NONBREEDING AND BREEDING SEASONS COMBINED

Winners	Losers					Totals	Rank
	31♂	3♀	10♀	1♀	18♂		
31♂		1	1	0	38	40	1
3♀	4		2	0	0	6	2
10♀	1	0		2	3	6	3
1♀	0	0	4		0	4	4
18♂	1	0	0	1		2	5

D.I.: 0.19 Grand Total: 58
h: 0.40

FIG. 1.—Dominance matrices for captive groups of opossums. Only agonistic interactions with clear winners or losers (fights or supplants) are included. The matrix for the nonbreeding season for group 1 includes only observation periods for which all five members were present. Data were pooled for nonbreeding and breeding seasons for group 3, because only 58 agonistic interactions were seen. Landau's *h* is independent of a priori ranking, and takes into account both "blanks" (dyads for which no interaction was seen) and "triangles" (nonlinear relationships among three or more individuals). Possible values for *h* range from 1.0 (perfect linearity) to zero (complete lack of hierarchy). The probability that relationships in a group will be assigned a high *h* by chance increases for small groups and cannot be calculated for groups of five or fewer. D.I. = number of wins occurring in the least frequent direction for each dyad summed over all dyads and expressed as a percentage of the total number of agonistic encounters; it is independent of the overall frequency of interactions. Low D.I. indicates a high degree of asymmetry or predictability in the outcome of interactions.

activity during the study (Fig. 2a). Three potentially confounding variables, temperature, time of night, and number of opossums per group, together accounted for only 6% of the variation in frequency of interactions ($R^2 = 0.059$); temperature did not contribute significantly to the variance explained by the regression model. The mean number of interactions overall per period and general activity both increased with the onset of breeding in early January, dropped nearly to nonbreeding season levels in February, and increased again in March and April.

The peak frequency of social interactions overall associated with the onset of estrus in January was attributable not only to an increase in sexual interactions, but to high levels of neutral or affiliative and agonistic encounters (Fig. 2b). All three interaction types declined in February, although the frequency of neutral or affiliative interactions remained elevated relative to nonbreeding-season levels. Neutral or affiliative interactions increased again in April, whereas agonistic encounters returned to nonbreeding season levels and remained relatively low. Sexual encounters were consistently less frequent than neutral or affiliative and agonistic interactions, and declined steadily as the breeding season progressed.

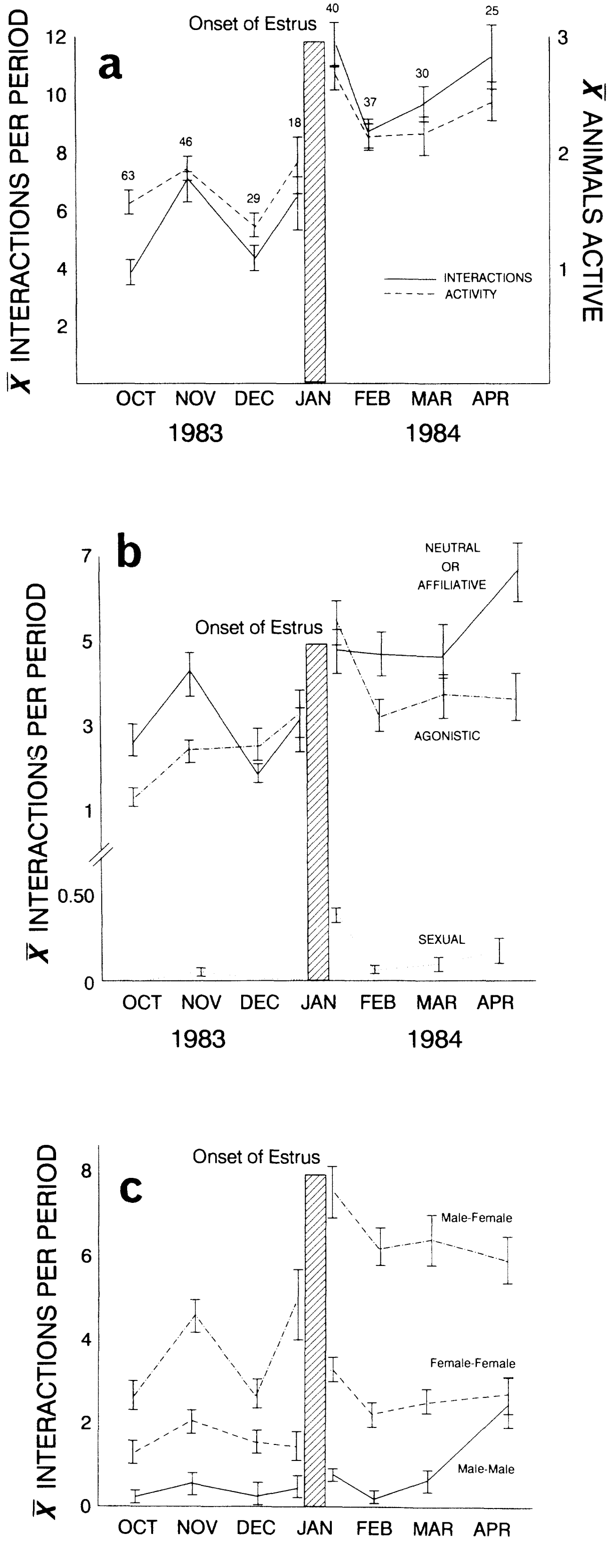
a
X̄ INTERACTIONS PER PERIOD
12
10
8
6
4
2
Onset of Estrus
63
46
29
18
40
37
30
25
INTERACTIONS
ACTIVITY
3
2
1
X̄ ANIMALS ACTIVE
OCT NOV DEC JAN FEB MAR APR
1983
1984
b
X̄ INTERACTIONS PER PERIOD
7
5
3
1
0.50
0
Onset of Estrus
NEUTRAL OR AFFILIATIVE
AGONISTIC
SEXUAL
OCT NOV DEC JAN FEB MAR APR
1983
1984
c
X̄ INTERACTIONS PER PERIOD
8
6
4
2
0
Onset of Estrus
Male-Female
Female-Female
Male-Male
OCT NOV DEC JAN FEB MAR APR
1983
1984

TABLE 1.—*Observed and expected number of days on which nestboxes were occupied by 1, 2, 3, and ≥4 captive opossums. Chi-squares were calculated for goodness of fit to a Poisson distribution for each group;* $S^2 > X$ *and* $S^2/\bar{X} > 0$ *for all three groups (Zar, 1984).*

	Group					
	1		2		3	
Number of occupants	Observed	Expected	Observed	Expected	Observed	Expected
0	84	73.21	73	80.50	111	52.47
0	60	75.42	96	82.11	61	78.19
2	37	38.85	34	41.87	18	57.09
3	21	13.33	17	14.24	33	28.93
≥4	3	4.10	3	10.79	10	14.87
χ^2 (*d.f.* = 3)	9.53*		10.68**		97.70***	

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Male-female and female-female interactions increased sharply at onset of estrus (Fig. 2c), and both remained high relative to nonbreeding-season levels through the end of the study. Male-male interactions, in contrast, also increased in January, but returned to levels lower than those of the nonbreeding season until April.

Nestboxes were used by opossums in a significantly nonrandom fashion (Table 1), with groups of two or three animals aggregating continually during the resting period in all three groups. Members of group 1 all were found in a single box on two occasions; these were the only two instances that males were seen resting together. Male-female nesting associations were significantly more common than female-female associations ($\chi^2 = 9.85$, *d.f.* = 1, $P < 0.005$; with expected frequencies adjusted for the actual sex ratio in each group), accounting for 134 of 176 days (76%) on which box occupants were determined. Although nesting associations were distributed nonrandomly among all possible dyads in each group (tests of goodness of fit to a random distribution of associations among dyads resulted in χ^2s with $P < 0.001$ for all groups), there was no apparent correspondence between frequency of nesting associations and of neutral or affiliative interactions between particular individuals.

Nesting associations persisted throughout the study and during the warmer months, with no suggestion of a systematic relationship between indoor temperature and number of nesting associations. There was, however, a shift to female-female nesting associations in the second half of the study: during the nonbreeding season, 18 of 82 (22%) nesting associations were female-female; in the breeding season, 29 of 97 (30%) associations were female-female ($\chi^2 = 5.70$, *d.f.* = 1, $P < 0.025$). Although certain nestboxes were selected repeatedly by several group members, opossums generally did not select individual boxes.

Of five dominance matrices constructed, four generated Landau scores of ≥0.90 (Fig. 1), suggesting strongly linear dominance hierarchies (Appleby, 1984; Chase, 1974). Values of the directional inconsistency index were consistently <0.25 and averaged 0.18, indicating a high degree of unidirectionality of agonistic encounters. Females held the highest ranks in groups 1 and 2 in both nonbreeding and breeding seasons; a male was dominant in group 3. Despite shifts in dominance ranks overall between nonbreeding and breeding seasons in groups 1 and 2, the same females remained dominant in both these groups throughout the study. The dominance relationship between the two males in each group remained stable between seasons.

←

FIG. 2.—Variation in mean frequency of social interactions overall and mean number of animals active (a); mean frequency of social interactions by interaction type (b); and mean frequency of social interactions by sex of participants (c) in opossum groups. Data are for all three groups combined; bars represent standard errors. Numbers above bars in (a) indicate number of observation periods for that month; these were the same in (b) and (c).

Low-ranking animals generally were less vigorous and more likely to suffer from upper respiratory infections and bite wounds. When data were pooled for males and females, dominance was not significantly associated with average body weight ($r_s = -0.13$, *d.f.* = 14, $P > 0.05$; recall that dominants have lower ranks that subordinates), and was associated positively, but not significantly, with the total frequency of social interactions ($r_s = -0.39$, *d.f.* = 14, $P > 0.05$). Dominance was associated positively, but not significantly, with frequency of courtship by males ($r_s = -0.79$, *d.f.* = 5, $P > 0.05$), and with frequency of submission to courtship by females ($r_s = -0.58$, *d.f.* = 8, $P > 0.05$). An association between dominance and number of litters borne by females also was positive, but not significant ($r_s = 0.57$, *d.f.* = 8, $P > 0.05$). The only significant correlation that emerged between a possible indicator of fitness and social behavior was between average body weight and total number of interactions ($r_s = 0.62$, *d.f.* = 14, $P < 0.05$; data pooled for both sexes).

Discussion

Spontaneous social interactions among group-housed opossums at the densities employed in this study were predominantly nonagonistic or affiliative, rather than characterized exclusively by aggression or avoidance. The marked increase in social interactions of all types corresponding with the onset of breeding indicates that seasonal influences should be considered when describing opossum social structure, whether in captivity or in the wild.

Nesting patterns also were characterized by greater social tolerance than expected, except between males. Because groups were composed almost entirely of unrelated individuals this tolerance cannot be attributed to confining littermates together past the usual age of dispersal in the wild. Moreover, it is clear that occasional reports of den sharing cannot be explained simply by the need for warmth, as has been suggested (Fitch and Shirer, 1970; Pippitt, 1976; Yeager, 1936). Radiotelemetric data on *Didelphis* in Florida and Venezuela suggest that, although males may consort briefly with estrous females, den sharing by adult opossums occurs rarely in the wild (Ryser, 1990; Sunquist et al., 1987). The intolerance of adult males for one another observed in this study is consistent with the highly competitive nature of male-male interactions reported for natural populations of *Didelphis* during the breeding season (Austad and Sunquist, 1986; Ryser, 1990; Sunquist et al., 1987).

The capacity of captive opossums to form stable, hierarchical social relationships contrasts with some published generalizations about didelphids (Charles-Dominique, 1983). The dominance of females in four of five matrices constructed, however, agrees with the outcome of staged encounters of pairs of opossums described by Hayssen (1985) and McManus (1970). Although no significant association between dominance rank and mating success emerged, these results are consistent with the relationship between agonistic encounters, social dominance, and priority of access to mates recently described for wild opossums in Florida (Ryser, 1990).

Taken as a whole, this study corroborates a growing body of field data on space-use and social systems in the genus *Didelphis* and indicates that opossum social behavior is more complex than generally thought. The old notion that *Didelphis* is nomadic, with no well-developed home ranges, has been refuted (Austad, 1984; Fitch and Shirer, 1970; Gillette, 1980; Ryser, 1990; Sunquist et al., 1987; Telford et al., 1979). Overlap in home ranges and evidence for a well-developed system of chemical communication (Gardner, 1982; Holmes, 1987, 1990; Holmes Meisner, 1986; McManus, 1970; Schaffer, 1940) suggest higher encounter rates between conspecifics than previously suspected. Available food and environmental heterogeneity clearly influence population density and space use in this genus (Gardner, 1982). These factors also probably influence social structure, which may be flexible enough to allow high population densities when food is plentiful. Social flexibility, coupled with generalized food and den requirements, may help account for the opossum's success in urban and suburban habitats (Gardner, 1982; Hopkins, 1980; Hopkins and Forbes, 1979, 1980).

Acknowledgments

I am grateful to K. Foltz, P. Brewton, K. Henderson, C. Kamen, and J. Soster for help with animal care, data tabulation and coding, and to J. Harder of The Ohio State University for help with vaginal smears. S.

Vessey, M. Sunquist, and several anonymous reviewers greatly improved the manuscript. This project was supported by National Science Foundation Grant BNS-844141, the Association for Women in Science, Sigma Xi, and the Graduate College of Bowling Green State University.

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Submitted 5 September 1989. Accepted 28 May 1990.