



NATAL PHILOPATRY AMONG SOLITARY MAMMALS

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ABSTRACT

Although many studies treat the causes and consequences of dispersal in mammalian populations, less attention has been given to the individuals that do not leave their birthplaces. Yet natal philopatry, which we define as continued residence on the natal home range past the age of independence from the parents, occurs in virtually all gregarious mammals. We here document its widespread occurrence among solitary species as well. By studying the distribution of natal philopatry across various ecological and life-history regimes we attempt to identify its ultimate causes. The variables that emerge as possibly important include adult turnover rates, habitat saturation, spatial patchiness of resources, advantages of familiarity with the natal home range, and reliance on extensive home range "improvements" such as burrow systems or food caches.

The most interesting consequence of natal philopatry is the continued spatial association of kin into adulthood, a prerequisite for many phenomena common to gregarious species. Natal philopatry, however, is considerably more widespread than are social groups, and all mammalian taxa containing gregarious species also include solitary species that exhibit philopatry. These observations suggest that an important part of understanding how complex social groups have arisen is understanding the conditions that have led to natal philopatry.

INTRODUCTION

AMONG MOST mammals, juveniles leave their natal home ranges before sexual maturity and travel distances of a few tens of meters to hundreds of kilometers before becoming breeding residents. For much of this century, dispersal has been a subject of primary concern to field naturalists; as a result, the data on timing and maximum extent of dispersal are encyclopedic (Baker, 1978). In comparison to their dispersing conspecifics, those juveniles who remain at home have virtually escaped notice. It is the contention of this review that the evolutionary consequences of nondis-

persal are as significant as those of dispersal, and that their ultimate causes are of equal interest.

Selection might favor dispersing juveniles (or adults who encourage their dispersal) for many reasons. Among iteroparous species, nondispersing young may compete directly with parents for food, dens, or reproductive opportunities. Murray (1967) was among the first to argue that under these conditions, individuals may maximize their own reproductive success by dispersing. The early literature (e.g., Howard, 1960; Lidicker, 1962) further suggested that dispersers

might benefit through an increased frequency of encounters with members of the opposite sex, genetically more variable or heterozygous offspring, reduced levels of interference competition, or access to empty but suitable habitats.

More recently, Bengtsson (1978; see also Shields, 1982) has explored the extent to which problems of inbreeding depression should favor dispersal, and Packer (1979) and Greenwood, Harvey, and Perrins (1979) have documented inbreeding depression among nondispersing individuals. Hamilton and May (1977) have demonstrated theoretically that individual selection should favor the dispersal of propagules even in the absence of inbreeding depression (which does not occur in their model) and even in stable, saturated environments. For these and other reasons, Horn (1978) has argued that dispersal, "especially in the form of itinerant adolescence," should be favored even in "a crowded population of sedentary, long-lived adults" (p. 428). Despite these arguments, it is clear that many juvenile mammals remain within their natal home range past the age of independence, and sometimes continue to occupy it throughout their entire lives.

Nondispersal is a central characteristic of complex social groups in organisms as diverse as termites, communally breeding birds, and primates (Vehrencamp, 1979). Yet the data we will discuss indicate that nondispersal is not confined to "social" species, but is widespread among solitary mammals as well. Under what conditions, then, will selection favor nondispersal? What consequences does nondispersal have for the evolution of mammalian social systems? These two questions motivate our search for cross-species correlates—ecological, demographic, and behavioral—of "natal philopatry" in solitary mammals.

DEFINITIONS: PHILOPATRY AND RELATED PHENOMENA

Greenwood (1980) has termed species that are faithful to their natal and breeding site or group "philopatric." We define natal philopatry as an individual's continued use of its natal home range past the age of indepen-

dence from its parent(s). We emphasize that natal philopatry is not a single, unified phenomenon. Our definition furthermore excludes a variety of similar or related phenomena; for instance, it is more restrictive than those of Greenwood (1980) or Shields (1982). Our criteria for identifying cases of natal philopatry in the literature thus require some elaboration.

First, philopatry by our definition is attachment to a site, rather than to a conspecific individual or group of conspecifics. Many mammalian groups (though not all) are extended families, "social" species differing from solitary congeners in the length of time over which individuals remain associated with their parents (in most cases, their mother) (Eisenberg, 1977). In such situations juveniles are philopatric as well, but philopatry need not dictate life in groups.

Where individuals habitually live in close spatial association, the question, What conditions favor philopatry? can become confounded with another, What factors favor living in groups? Since the latter question has been discussed extensively elsewhere (e.g., Bertram, 1978), we will exclude gregarious species from this review and will concentrate on solitary mammals among which the young do not routinely forage with a parent after independence but nevertheless remain on the parent's home range.

"Solitary," as we use the term, thus refers to the spatial distribution of animals relative to each other, and not to their patterns of social interaction: solitary species are those whose members are usually found alone. An individual that forages alone may decrease its rate of interaction with conspecifics, but it need not decrease the number of individuals recognized and may still live within a complex social network. "Solitary" is the opposite not of "social" but of "gregarious" (Charles-Dominique, 1977a).

We hope that our data will make clear that any line drawn between "solitary" and "gregarious" is inherently arbitrary. For instance, we categorize the red fox as solitary, since foxes usually forage alone, although in some areas territories are shared by up to six adults that may use the same dens and frequently engage in amicable interactions (MacDonald, 1981). [See Table 1 for sci-

ific names of all species discussed in text.] On the other hand, we omit coyotes and jackals from our tables, since in some areas they form foraging groups (e.g., Bowen, 1981; MacDonald, 1979a). We attempt to standardize our categorizations by emphasizing spatial distribution during the animals' period of peak activity. For instance, the white-lined bat roosts in small colonies (Bradbury and Vehrencamp, 1976), but we include it as solitary because individuals forage independently at night.

Since interactions between philopatric offspring and their parents can continue in some degree throughout life, independence from parents is ambiguous. We define independence as beginning when offspring cease to forage in spatial association with the mother. Thus we consider natal philopatry to occur among bushbabies if they do not leave their mother's home range when they begin foraging alone, even though nondispersing juveniles may continue, at least occasionally, to share nests with their mothers (e.g., Charles-Dominique, 1977a). In particular, we do not intend to imply that all parental influence on the reproductive success of their offspring terminates at "independence."

To establish the extent of philopatry ideally requires that one follow numbers of individually identified juveniles longitudinally from birth through adulthood. Few studies of solitary mammals have been designed to acquire such information, so that in most cases the information available is anecdotal. In some cases, philopatry has been inferred in the field, for instance, by noting "old" and "young" individuals that share home ranges, or individuals with similar coat color variants that use neighboring areas. We believe that despite the difficulties of observing solitary mammals, many field observers have indeed collected the data necessary to assess philopatric tendencies, but have not published them, and instead have documented only the frequency of long-distance dispersal or the duration of the spatial association between offspring and parent. We hope that this review will stimulate the publication of such data. Meanwhile, we have been forced to adopt a set of criteria that distinguish between inferential and anecdotal evidence

for philopatry (where the number of longitudinally followed juveniles is very small [<5] or is unstated) on one hand, and evidence that allows at least a crude estimate of the frequency of philopatry (studies with data from >5 juveniles), on the other.

The nature of the available information may introduce a bias into our summary tables, since when philopatry is not mentioned we cannot conclude that it did not occur. In addition, since we define philopatry as a failure to disperse from the natal home range, we cannot conclude that lack of dispersal from a local population (e.g., Lidicker, 1975; Tamarin, 1980; Gaines and McClenaghan, 1980) is equivalent to philopatry.

In response to these problems, we have chosen to list all species in which we have found any evidence for philopatry, with the admission that where data are anecdotal or inferential, philopatry may not be the norm. The skeptic may prefer to view our summary tables as lists of species in which the potential for natal philopatry has been demonstrated, though its significance for the species concerned may still be uncertain.

A phenomenon similar to philopatry in some of its consequences can occur when vacancies in home ranges neighboring the parents' are common. Offspring may then vacate the natal area but settle immediately adjacent to it, and thus near to parents or sibs. We consider such offspring to have dispersed. This phenomenon can be difficult to distinguish from philopatry, however, when information on home-range boundaries and turnover is not precise. When in doubt, we have designated philopatry as "probable."

Sharing or donating space to the offspring always has the potential of reducing future parental reproductive success. How much these behaviors actually do so will depend, among other things, on the timing of eventual juvenile dispersal (if the young are not philopatric throughout life) and on the likelihood of parental survival. If the parent dies, philopatry results in inheritance of the parental home range. Although our definition of philopatry requires neither lifetime site-faithfulness nor guaranteed parental survival, the evolution of the phenomenon is more interesting when both occur. We attempt to document the persistence of natal

TABLE 1
Taxonomic distribution of natal philopatry^{1,4}

Species	Philopatry persists: ²			Offspring breed on natal area: ³			References
	Beyond independence	Beyond parents' next breeding episode	Beyond minimum reproductive age	While same-sexed parent is alive	After disappearance of same-sexed parent	Status of parent unknown	
Marsupialia							
Didelphidae							
<u>Didelphis virginiana</u> Virginia opossum	A/A	A/-	A/-				Gillette, 1980; Llewellyn and Dale, 1964; Sanderson, 1961
Phalangeridae							
<u>Trichosurus vulpecula</u> brush-tailed possum	C/C	C/O	C/O	Y/I			Dunnett, 1964; R. How, 1978, pers. commun.
<u>T. caninus</u> mountain possum	C/C	C/C	A/A		Y/-		R. How, 1981, pers. commun.
<u>Petaurus breviceps</u> sugar glider	C/C	N/N	N/N				Smith, 1980
<u>Gymnobelideus leadbeateri</u> leadbeaters possum	C/C	C/C	O/O		Y/Y		Smith, 1980
Phascolarctidae							
<u>Phascolarctos cinereus</u> koala	O/O	O/O	O/O				G. Gordon, pers. commun.
Macropodidae							
<u>Setonix brachyurus</u> quokka	A	A	A				Dunnett, 1962; Holsworth, 1967
Insectivora							
Macroscelididae							
<u>Rhynchocyon chrysopygus</u> golden-rumped elephant shrew	C						Rathbun, 1979
<u>Elephantulus rufescens</u> rufous elephant shrew	C	A	A				Rathbun, 1979
Soricidae							
<u>Sorex araneus</u> common shrew	P						Crowcroft, 1957; Shillito, 1963
Talpidae							
<u>Talpa europaea</u> European mole	A/A						Godfrey, 1957
Chiroptera							
Emballonuridae							
<u>Saccopteryx bilineata</u> white-lined bat	A/A	O/P	O/P				Bradbury and Vehrencamp, 1976
Phyllostomatidae							
<u>Phyllostomus hastatus</u> spemannose bat	C/C	N/N	N/N				McCracken and Bradbury, 1981
Primates							
Tupaiaidae							
<u>Tupaia glis</u> tree shrew	I2/-						Kawamichi and Kawamichi, 1979
Lemuridae							
<u>Microcebus coquereli</u> Coquerel's mouse lemur	-/A						Pages, 1980
<u>M. murinus</u> lesser mouse lemur	I1/-	I1/-	I1/-				Martin, 1972; Charles- Dominique 1977a
<u>Lepilemur mustelinus</u> sportive lemur	I1/-	I1/-	I1/-	I1/-			Charles-Dominique and Hladik, 1971
Lorisiidae							
<u>Galago crassicaudatus</u> thick-tailed bushbaby	A/C	A/C	A/C	Y/-			Bearder and Doyle, 1974; A. Clark, 1973, pers. commun.
<u>G. demidovii</u> Demidov's bushbaby	C/C	C/N	C/N	I/-			Charles-Dominique, 1972, 1977a

TABLE 1 (Continued)
Taxonomic distribution of natal philopatry^{1,4}

Species	Philopatry persists: ²			Offspring breed on natal area: ³		References
	Beyond independence	Beyond parents' next breeding episode	Beyond minimum reproductive age	While same-sexed parent is alive	After disappearance of same-sexed parent	
<i>C. senegalensis</i> lesser bushbaby	C/O	C/O	C/O	Y/-		Bearder and Martin, 1980; Charles-Dominique and Bearder, 1979
<i>C. alleni</i> Allen's bushbaby	A/-	A/-	A/-			Charles-Dominique, 1977a, b
<i>Periodictus potto</i> potto	A/A	A/A	A/-	-/Y		Charles-Dominique, 1974
<i>Tarsius spectrum</i> spectral tarsier	A/A	A/A	A/A	I/-		MacKinnon and MacKinnon, 1981
<i>I. bancanus</i> western tarsier	I3/-					Fogden, 1974
<i>Bradypodidae</i> <i>Bradypus tridactylus</i> three-toed sloth	A/-					Montgomery and Sunquist, 1978
<i>Chlorocebus princeps</i> pink	C/C	P/P	P/P		-/I	Smith, 1978, 1981, Smith and Ivins, in press
<i>Oryctolagus cuniculus</i> European rabbit	C/-	C/O	C/O		Y/-	Mykytowycz, 1959, 1960; Young, Strecker and Emlen, 1950
<i>Spermophilus richardsoni</i> Richardson's ground squirrel	C/C	C/O	C/O		Y/-	Michener, 1979, 1980; Michener and Michener, 1977
<i>S. tereticaudus</i> round-tailed ground squirrel	C/-	C/-	C/-			Dunford, 1977a
<i>S. beldingi</i> Belding's ground squirrel	C	P/N	P/N			Sherman, 1980; Turner, 1972
<i>S. beecheyi</i> Beechey ground squirrel	P/O	P/N	P/N			Evans and Holdreid, 1943; Dobson, 1979
<i>S. tridecemlineatus</i> thirteen-lined ground squirrel	C/O	C/O	C/O			Evans, 1951; McCarley, 1966; Schwagmeyer, 1980
<i>S. variegatus</i> rock squirrel	C/C	II/-	II/-			Johnson, 1981
<i>S. armatus</i> Santa ground squirrel	A/-	A/-	A/-			Slade and Balph, 1974
<i>Neotoma striatus</i> eastern chipmunk	V/O	V/O	V/O		Y/-	Elliott, 1978; Yahner, 1978
<i>Sciurus carolinensis</i> gray squirrel	C/C	C/C	C/C	Y/Y		Thompson, 1978a, b
<i>Tamiasciurus hudsonius</i> red squirrel	A/A					Layne, 1954; Smith, 1968
<i>T. douglasii</i> Douglas squirrel	C					Smith, 1968
<i>Reithrodon chrysomelas</i> bush squirrel	A/A	A/A				Viljoen, 1977
<i>Perognathus rufus</i> yellow-cheeked pocket gopher	P					Smolen, Genoways and Baker, 1980

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	Beyond independence	Beyond parents' next breeding episode	Beyond minimum reproductive age	While same-sexed parent is alive	After disappearance of same-sexed parent	Status of parent unknown		
Marsupialia								
Didelphidae								
<u>Didelphis virginiana</u> Virginia opossum	A/A	A/-	A/-				Gillette, 1930; Llewellyn and Dale, 1964; Sanderson, 1961	<u>G. senegalensis</u> lesser bushb
Phalangeridae								
<u>Trichosurus vulpecula</u> brush-tailed possum	C/C	C/O	C/O	Y/I			Dunnett, 1964; R. How, 1978, pers. commun.	<u>G. allenii</u> Allen's bush
<u>T. caninus</u> mountain possum	C/C	C/C	A/A		Y/-		R. How, 1981, pers. commun.	<u>Perodicticus potto</u> potto
<u>Petaurus breviceps</u> sugar glider	C/C	N/N	N/N				Smith, 1980	<u>Tarsius Spectr</u> spectral tars
<u>Cynobalideus leadbeateri</u> leadbeaters possum	C/C	C/C	O/O	Y/Y			Smith, 1980	<u>T. bancanus</u> western tars
Phascolarctidae								
<u>Phascolarctos cinereus</u> koala	O/O	O/O	O/O				G. Gordon, pers. commun.	<u>Uromastyx</u> three-toed sl
Macropodidae								
<u>Setonix brachyurus</u> quokka	A	A	A				Dunnett, 1962; Holsworth, 1967	<u>Uromastyx</u> morphe
Insectivora								
Macroscelididae								
<u>Rhynchocyon chrysopygus</u> golden-rumped elephant shrew	C						Rathbun, 1979	<u>Chelonis princeps</u> pike
<u>Elephantulus rufescens</u> rufous elephant shrew	C	A	A				Rathbun, 1979	<u>Lepus</u> European rabb
Soricidae								
<u>Sorex araneus</u> common shrew	P						Crowcroft, 1957; Shillito, 1963	<u>Sciurus</u> Richardson's squirrel
Talpidae								
<u>Talpa europaea</u> European mole	A/A						Godfrey, 1957	<u>S. tereticaudus</u> round-tailed squirrel
Chiroptera								
Emballonuridae								
<u>Saccopteryx bilineata</u> white-lined bat	A/A	O/P	O/P				Bradbury and Vehrenkamp, 1976	<u>S. bedfordi</u> Bedford's ground squirrel
Phyllostomidae								
<u>Phyllostomus hastatus</u> spemann's bat	C/C	N/N	N/N				McCracken and Bradbury, 1981	<u>S. tridecemlineatus</u> thirteen-lined squirrel
Primates								
Tupaiaidae								
<u>Tupaia glis</u> tree shrew	I2/-						Kawanichi and Kawanichi, 1979	<u>S. variegatus</u> rock squirrel
Lemuridae								
<u>Microcebus coquereli</u> Coquerel's mouse lemur	-/A						Pages, 1980	<u>S. armatus</u> Santa ground squirrel
<u>M. murinus</u> lesser mouse lemur	II/-	II/-	II/-				Martin, 1972; Charles-Dominique, 1977a	<u>S. striatus</u> eastern chipmunk
<u>Lepilemur mustelinus</u> sportive lemur	II/-	II/-	II/-	II/-			Charles-Dominique and Hladik, 1971	<u>S. carolinensis</u> gray squirrel
Lorisidae								
<u>Galago crassicaudatus</u> thick-tailed bushbaby	A/C	A/C	A/C	Y/-			Bearder and Doyle, 1974; A. Clark, 1978, pers. commun.	<u>S. sciurus</u> red squirrel
<u>G. demidovi</u> Demidov's bushbaby	C/C	C/N	C/N	I/-			Charles-Dominique, 1972, 1977a	<u>S. lasiurus</u> black squirrel

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<i>S. senegalensis</i> Lesser bushbaby	C/O	C/O	C/O	Y/-			Bearder and Martin, 1980; Charles-Dominique and Bearder, 1979
<i>S. alleni</i> Allen's bushbaby	A/-	A/-	A/-				Charles-Dominique, 1977a, b
<i>Perodictus potto</i> Potto	A/A	A/A	A/-	-/Y			Charles-Dominique, 1974
<i>Caplorhinus</i> Spectral tarsier	A/A	A/A	A/A	I/-			MacKinnon and MacKinnon, 1981 Fogden, 1974
<i>Caplorhinus</i> Western tarsier	I3/-						
<i>Arctocebus</i> Three-toed sloth	A/-						Montgomery and Sunquist, 1978
<i>Caplorhinus</i> Princeps	C/C	P/P	P/P	-/I			Smith, 1978, 1981, Smith and Ivins, in press
<i>Caplorhinus</i> European rabbit	C/-	C/O	C/O			Y/-	Mykytowycz, 1959, 1960; Young, Strecker and Emlen, 1950
<i>Spermophilus richardsoni</i> Richardson's ground squirrel	C/C	C/O	C/O			Y/-	Michener, 1979, 1980; Michener and Michener, 1977 Dunford, 1977a
<i>S. tereticaudus</i> Round-tailed ground squirrel	C/-	C/-	C/-				Sherman, 1980; Turner, 1972
<i>S. beeldingi</i> Belding's ground squirrel	C	P/N	P/N				Evans and Holdenreid, 1943; Dobson, 1979
<i>S. beecheyi</i> Beechey ground squirrel	P/O	P/N	P/N				Evans, 1951; McCarley, 1966; Schwagmeyer, 1980
<i>S. tridecemlineatus</i> Thirteen-lined ground squirrel	C/O	C/O	C/O				Johnson, 1981
<i>S. variegatus</i> Rock squirrel	C/C	I1/-	I1/-				Slade and Balph, 1974
<i>S. armatus</i> Florida ground squirrel	A/-	A/-	A/-			Y/-	Elliott, 1978; Yahner, 1978
<i>Thomomys talpae</i> Eastern chipmunk	V/O	V/O	V/O				Thompson, 1978a, b
<i>Thomomys carolinensis</i> Gray squirrel	C/C	C/C	C/C	Y/Y			Layne, 1954; Smith, 1968
<i>Thomomys hudsonius</i> Red squirrel	A/A						Smith, 1968
<i>Thomomys</i> Bush squirrel	C						Viljoen, 1977
<i>Thomomys</i> Pocket	P						Smolen, Genoways and Baker, 1980

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Heteromyidae							
<u>Dipodomys merriami</u> Merriam's kangaroo rat	P/P	P/P	P/P			Y/Y	Jones, 1982
<u>D. spectabilis</u> bannertailed kangaroo rat	C/C	O/O	C/C	Y/Y	Y/Y	Y/Y	Jones, 1982
Castoridae							
<u>Castor canadensis</u> beaver	C/C	C/C	O				Bradt, 1938; Townsend, 1953; Beer, 1955
Cricetidae							
<u>Peromyscus maniculatus</u> prairie deer mouse	C/C	C/C	C/C	Y/-		Y/Y	Howard, 1949
<u>Microtus agrestis</u> field vole	C	-/N	-/N				Myllymäki, 1977a, b
<u>M. arvalis</u> common vole	C/C	C/N	C/N	Y/-			Frank, 1957
<u>M. montanus</u> montane vole	C	C					Jannett, 1978, 1980
<u>M. pennsylvanicus</u> meadow vole	II/-	II/-	II/-				Madison, 1980
<u>M. ochrogaster</u> prairie vole	C/C	C/C	C/C	Y/-	Y/-		L. Getz, pers. commun.
<u>Arvicola terrestris</u> water vole	C/A	C/A	C/A	Y/N	Y/-		Airolidi, 1978; Leura, 1976, 1980
<u>Neotoma fuscipes</u> dusky-footed woodrat	C/C	-/O	C/O	-/Y		Y/Y	Linsdale and Tevis, 1951
<u>N. floridana</u> eastern woodrat	A/C	A					Fitch and Rainey, 1956; Pearson, 1952
<u>Psammomys obesus</u> sand rat	C/C	O/O	O/O				Daly and Daly, 1975
<u>Odonthra zibethica</u> muskrat	P	P					Errington, 1939
Rhizomyidae							
<u>Tachyoryctes splendens</u> root-rat	II						Jarvis, 1973
Bathyergidae							
<u>Heliohobius argentocinereus</u> silky blesmol	II	II	II				Jarvis and Sale, 1971
Muridae							
<u>Mus musculus</u> house mouse	C		C		Y		Anderson, 1967, 1970; Crowcroft and Rowe, 1963; Eibl-Eibesfeldt, 1950; Fitzgerald, Kari and Moller, 1981; Lidicker, 1976; Rowe and Redfern, 1969; Selander, 1970
<u>M. oubanqui</u>	I3	I3	I3				Genest-Villard, 1973
<u>Rattus norvegicus</u> Norway rat	A/A						Hardy and Taylor, 1980
Hystriidae							
<u>Atherurus africanus</u> brush-tailed porcupine	I2	I2	I2				L. Emmons, pers. commun.
Erithizontidae							
<u>Erithizon dorsatus</u> American porcupine	A/-						Marshall, Gullion and Schevals, 1962
Dasyproctidae							
<u>Dasyprocta punctata</u> agouti	A/-	A/-	A/-	Y/-			Galef and Clark, 1975; Smythe, 1978

TABLE 1 (Continued)
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		Beyond independence	Beyond parents' next breeding episode	Beyond minimum reproductive age	While same-sexed parent is alive	After disappearance of same-sexed parent	Status of parent unknown	
	Caviidae							Rood, 1970
	<u>Microcavia australis</u> desert cavy	C	O/-	O/-	Y/-			
	Carnivora							
	Canidae							Ables, 1969; Follman, 1973; MacDonald, 1980a, 1981; Phillips et al., 1972; Sergeant, 1972; Sheldon, 1950; Storm, 1972; Storm et al., 1976; von Schantz, 1981a, b
	<u>Vulpes vulpes</u> red fox	V/A	V/A	V/A	Y/-			Egoscue, 1956, 1975; Golightly, 1981; Morrell, 1972
	<u>Vulpes macrotis</u> kit fox	V/-	II/-	II/-	I/-			Follman, 1973; Trapp, 1978
	<u>Urocyon cinereoargenteus</u> gray fox	O/I	I/-			Y/-		Hersteinsson and MacDonald, 1981; L. Eberhardt, pers. commun.
	<u>Alopex lagopus</u> arctic fox	A/-	A/-	A/-				Lamprecht, 1979; J. Malcolm, pers. commun.
	<u>Otocyon megalotis</u> bat-eared fox	II/-	II/-	II/-	I/-			Gauthier-Pilters, 1967
	<u>Fennecus zetta</u> fennec	II/-	II/-					Brady, 1979
	<u>Cerdocyon thous</u> crab-eating fox	I3/-						
	Ursidae							Jonkel and Cowan, 1971; Lindsey and Meslow, 1977; Rogers, 1977
	<u>Ursus americanus</u> black bear	C/C	C/N	C/N	Y/-			Craighead and Craighead, 1972; Pearson, 1975
	<u>U. arctos</u> grizzly bear	C/A	A/A	A/-				Fritzell, 1978; Rangen, 1954; Mech and Turkowski, 1966; Schneider, Mech and Tester, 1971; Steuwer, 1943
	Procyonidae							
	<u>Procyon lotor</u> raccoon	C/C	A/A	A/N	Y/-			Ahnlund, 1980; Kruuk, 1978a, pers. commun.; Neal, 1977
	Mustelidae							Messick and Hornocker, 1981
	<u>Meles meles</u> European badger	A/A	A/A	A/A				Allen, 1939; Houseknecht and Tester, 1979; Verts, 1957; A. Sergeant, et al., in press
	<u>Taxidea taxidea</u> American badger	O/O	O/O	N/N				Erlinge, 1977; E. Simms, 1979
	<u>Mephitis mephitis</u> striped skunk	II/-						Gerrell, 1970
	<u>Mustela erminea</u> ermine	C/C	C/-	C/-	Y/-			Charles-Dominique, 1978
	<u>M. vison</u> mink	A/-						Waser, unpub.
	Urotridae							
	<u>Nandinia binotata</u> palm civet	C/N	C/N	N/N				
	<u>Ichneumia albicauda</u> white-tailed mongoose	A/A	II,2/-	II,2/-	I/-			

C=common; A=anecdotal

TABLE 1 (Continued)
Taxonomic distribution of natal philopatry^{1,4}

Species	Philopatry persists: ²			Offspring breed on natal area: ³			References
	Beyond independence	Beyond parents' next breeding episode	Beyond minimum reproductive age	While same-sexed parent is alive	After disappearance of same-sexed parent	Status of parent unknown	
<i>Herpestes sanguineus</i> slender mongoose	A/A	A/N	A/N		Y/-		Rood and Waser, 1978
<i>H. auropunctatus</i> small Indian mongoose	I1/-	I1/-					Gorman, 1979; Lloyd-Jones, 1953; D. Nellis, pers. commun.
<i>H. ichneumon</i> Egyptian mongoose	I3/-						Fuente, 1972
Hyenidae							
<i>Hyaena brunnea</i> brown hyaena	C/C	C/C	C/C		Y/-		Mills, 1978, 1982; Owens and Owens, 1978, 1979
<i>H. hyaena</i> striped hyaena	I1/-	I3/-					Kruuk, 1976; MacDonald, 1978; Rieger, 1981
Felidae							
<i>Felis domesticus</i> housecat	C/C	C/C	C/O		Y/-		Dards, 1978; Laundre, 1977; Liberg, 1980; MacDonald and Apps, 1978; Pascal, 1980
<i>F. concolor</i> puma	O/O	N/N	N/N				Seidensticker, et al., 1973
<i>F. serval</i> serval	N/A						A. Geartsema, pers. commun.
<i>Acinonyx jubatus</i> cheetah	C/C	C/O	C/O	Y/N	Y/-	Y/N	Frame and Frame, 1977, 1981
<i>Panthera pardus</i> leopard	A/-	I1/-					Bertram, 1974; Muckenhirn and Eisenberg, 1973
<i>P. tigris</i> tiger	A/A	A/-	A/-		Y/-		Schaller, 1967; Sunquist, 1981
<i>P. onca</i> jaguar	A/-						Schaller, 1980
<i>Lynx rufus</i> lynx	A	N/N	N/N				Bailey, 1974, 1981
Artiodactyla							
Cervidae							
<i>Alces alces</i> moose	N/N	N/N	N/N				Geist, 1971
Tragulidae							
<i>Hyemoschus aquaticus</i> chevrotain	C/C	A/A	A/A		I/-		Dubost, 1978
Bovidae							
<i>Cephalophus monticola</i> blue duiker	C/C	C/C	C/C		Y/Y		Dubost, 1980
<i>Muntiacus reevesi</i> muntjac	A/-	A/-	A/-				Dubost, 1970
<i>Madoqua kirkii</i> Kirk's dikdik	N/N	N/N	N/N				Hendrichs, 1975
<i>Tragelaphus scriptus</i> bushbuck	I1/-	I1/-	I1/-		I/-		Waser, 1971
<i>Redunca arundinum</i> mountain reedbuck	A/A	A/A					Jungius, 1970

Notes: ¹Data for female offspring precede slash; data for male offspring follow it. A single entry indicates that sexes were not distinguished. Absence of an entry indicates the phenomenon has not been reported, though this may simply reflect lack of data.

²Frequency of natal philopatry: C = common, data on ≥ 5 individuals, nondispersal in $> 20\%$. V = variable, data on ≥ 5 individuals from two or more populations, nondispersal "common" in one and "occasional" or "none" in another. O = occasional, data on > 5 individuals, nondispersal in $\leq 20\%$. N = none, data on > 5 individuals, all disperse. A = anecdotal, philopatry reported, but sample size is < 5 individuals or unstated. I = inferred from indirect evidence. I1: author reports large/small or old/young individuals together or in clustered dens or home ranges; alternatively, author reports several same-aged young adults in clustered home ranges. I2: author reports "exploded groups," "tribes," or "clans" of

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TABLE 1 (Continued)

individuals sharing a common home range. 13: author infers philopatry on other or unstated grounds. P = probable, young "remain in natal area" but author does not indicate whether they are actually using the natal home range. -- = data do not exist or are insufficient to allow placement in the above categories.

Offspring breed on natal area: Y = yes. I = inferred by author. N = no. -- = no data.

The following taxa do not appear since well-studied species are all gregarious: Perissodactyla; Proboscidea; Suidae, Tayassuidae, Camelidae, Antilocapridae (Artiodactyla). The following taxa do not appear as data are lacking: Monotremata; Pholidota; Cetacea; Pinnipedia; Tubulidentata; Sirenia; Pedetidae, Gliridae, Zapodidae, Dipodidae (Rodentia); Hippopotamidae, Giraffidae (Artiodactyla).

References

- Aood and Waser, 1974
 Gorman, 1979; Lloyd-Jones, 1953; D. Nellis, pers. comm.
 Fuente, 1972
 Mills, 1978, 1982; Owens and Owens, 1978, 1979
 Kruuk, 1976; MacDonald, 1978; Rieger, 1981
 Dards, 1978; Landre, 1977; Liberg, 1930; MacDonald and Apple, 1978; Pascal, 1950
 Seidensticker, et al., 1973
 A. Geertsema, pers. commun.
 Frame and Frame, 1977, 1981
 Bertram, 1974; Muckenhirn and Eisenberg, 1973
 Schaller, 1967; Sunquist, 1981
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 Bailey, 1974, 1981
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 Dubost, 1978
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 Hendrichs, 1975
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 I = inferred from individuals together or in same-aged young adults
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philopatry, relative to important reproductive events, as an indicator of the extent to which parents of philopatric offspring might be forgoing their own future reproduction.

THE TAXONOMIC DISTRIBUTION OF NATAL PHILOPATRY

Natal philopatry is widespread, occurring in taxa as divergent as edentates and antelopes (see Tables 1,2). The ubiquity with which it has been observed is all the more striking, given the rarity of studies that follow more than a handful of individuals of known parentage to adulthood. In only a few populations with reasonable sets of data are all offspring reported to disperse.

Philopatry in Taxa with Gregarious Members Carnivores

A striking feature of the data as a whole is the widespread distribution of natal philopatry among taxa that also contain gregarious species. The canids provide an excellent illustration. Whereas red foxes are solitary foragers and usually live as pairs within non-overlapping territories, even the earliest field studies suggested tantalizing exceptions. For instance, Sheldon (1950) reported cases of two litters raised together in a single den, as well as cases of dens shared by nursing and "barren" females. Sheldon also reported a case of female philopatry—a pup tagged in 1947 was recaptured within 1/5 mile a year and a half later.

Sheldon (1950) did not imply that female den-sharing and nondispersal were related, but more recent studies suggest that to be the case. Ables (1969) followed a red fox family that included a male and female who continued to use their natal dens until at least three years of age, as well as two of the

female's daughters who used their natal dens as adults.

Follman (1973) described a red fox "territory" used by an old, a middle-aged, and a young female, along with a male; both older females reproduced during the study, and they denned communally. Although these four animals did not use space identically, they evidently tolerated each other within a common boundary, across which other foxes rarely penetrated.

MacDonald (1980a, 1981) found that 16 radiotagged adults each occupied one of five nonoverlapping ranges, which they shared with up to five other adults. MacDonald suggested that the females that share a range are related, on the basis of observations of philopatry as well as of coat color and other "family resemblances." MacDonald's (1981, p. 925) "impression of fox groups . . . is of well integrated, social communities, even if their members spend much of their time out of immediate physical contact."

It seems likely that variations on this theme will be common among canids. For instance, den-sharing by female pairs, inferred on various grounds to be mother and daughter, has been reported in the kit fox (Egoscue, 1956, 1975), the arctic fox (Hervestinnsson and MacDonald, 1981), and the bat-eared fox (Reynolds, 1976; J. Malcolm, pers. commun.). Thus there are no firm dividing lines among the pair-territories with occasional philopatry exhibited in some fox populations, the group ranges shared by philopatric but independent kin in others, the small matrilineal groups of some coyotes and jackals (Bekoff and Wells, 1980; Bowen, 1981; Moehlman, 1979), and the permanent family groups of wolves (Mech, 1970)—indeed, variation along this continuum can occur among populations within species (e.g., Kleiman and Brady, 1978; MacDonald, 1978, 1979a).

Parallel examples occur in all carnivore families with gregarious members: procyonids, viverrids, hyaenids, and felids (Table 1). All contain species that live in groups, generally based on matrilineal. Among the viverrids, female palm civets forage in their mothers' ranges until they mature at two years of age, and so three successive cohorts may cohabit (Charles-Dominique, 1978). Young white-tailed mongooses forage independently within their natal range through at least their first year. The adult females den solitarily but live in "clans," sharing a home range with presumed relatives, and excluding non-clan individuals (Waser, unpub.). Among the hyaenids, brown hyaenas forage solitarily, but in some areas most juveniles of both sexes live at least their first three years on their natal range; males then frequently but not always disperse (Mills, 1982; but see Owens and Owens, 1979).

Particularly striking are data from solitary felids. Cheetah cubs remain with their mothers from 14 to 18 months, then forage in sibling groups (Frame and Frame, 1981). By two years of age, all young females leave their sibling groups but remain within the mothers' home ranges. Most daughters continue to share their mother's range throughout life, and often reproduce there, though mother and daughter avoid each other.

Compared with most felids, feral housecats are ideal subjects for long-term studies of individual life histories, and their potential contribution to the understanding of philopatry is beginning to be exploited. Among farm cats, female philopatry is associated with social tolerance, simultaneous reproduction, and even shared suckling within matrilineal, whereas hunting remains a solitary affair (Laundré, 1977; MacDonald and Apps, 1978). In a high-density cat population in the Plymouth (England) dockyards, Dards (1978) found females sharing family ranges with little overlap among groups; moreover, 9 out of 20 of the young males she studied did not disperse even as yearlings. Shared home ranges within matrilineal have been reported among cats in areas far from human mutualists (Liberg, 1980; Pascal, 1980). Unfortunately, field studies of the likely ancestors of domestic cats are virtually nonexistent, though *Felis libyca* can be

readily followed in some study sites (Waser, pers. obs.).

Primates

The great majority of primate genera are gregarious, and groups in nearly all species are matrilineal. Work on prosimians demonstrates that an even more general primate characteristic is female philopatry per se, resulting in clusters of related females in overlapping home ranges. In every species of bushbaby that has been investigated, mothers shared home ranges (and sometimes nests) with their grown daughters. The extent of interaction and the proportion of nondispersing juveniles varied among populations (Bearder and Doyle, 1974; Charles-Dominique, 1977b; Clark, 1978). Similar phenomena have been described in other prosimians (Table 1). Charles-Dominique (1977b) has already noted the similarity in patterns of interaction and spacing among primates (e.g., bushbabies) and solitary carnivores (e.g., palm civets).

A related phenomenon has been reported in several primates living in small monogamous families. Among gibbons and siamangs, the offspring are eventually isolated in a peripheral subset of the parental group's home range, and the parents then avoid the allocated territory (Aldrich-Blake and Chivers, 1973; Tenaza, 1975; Chivers and Raemakers, 1980). Tilson (1981), reviewing the fates of maturing Kloss's gibbons, *Hylobates klossi*, found that 7 out of 8 juveniles of both sexes eventually established themselves on or immediately adjacent to their natal range by one of three routes: by establishing a new territory, with parental assistance, on the periphery of their parents'; by emigrating to an immediately adjacent group upon the death of one of its adults; or by replacing one of its own parents. Tilson suggested that the odds are against a juvenile's successful establishment in a breeding group not immediately adjacent to its parents. Although maturing animals might simply have better information about nearby openings, Tilson's observations suggest that direct parental aid, usually in the form of annexing space, is necessary. It would not be surprising if similar phenomena were discovered in monogamous neotropical monkeys.

Social groups consist of unthree taxa pro matrilineal in g deer (*Odocoileus* Tomich, 1958) (Darling, 1937 sill, 1979)]. W us), which are a erate daughter than a year pas (Palmer, 1951 1970); larger g reflect greater 1977). Roe dee are also relativ and remain th family area (K

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Ungulates

Social groups in many ungulate species consist of unrelated animals, but at least three taxa provide exceptions. Groups are matrilineal in gregarious cervids ([e.g., mule deer (*Odocoileus hemionus*) (Linsdale and Tomich, 1958) and red deer (*Cervus elephas*) (Darling, 1937; Guinness, Hall, and Cocke-sill, 1979)]. White-tailed deer (*O. virginian-us*), which are at least seasonally solitary, tol-erate daughters on the natal range more than a year past their reproductive maturity (Palmer, 1951; Hawkins and Klimstra, 1970); larger groups, in some habitats, may reflect greater natal philopatry (Hirth, 1977). Roe deer females (*Capreolus capreolus*) are also relatively solitary, but may breed and remain their entire lives in the same family area (Kurt, 1968).

A more extensive continuum of social structures involving philopatry appears to exist among the tragelaphine antelopes. Although some species form permanent matrilineal groups, the lesser kudu (*Tragelaphus imberbis*) and the nyala (*T. angasi*) form only small and temporary associations. Neverthe-less, females often share home ranges with their close female relatives (Leuthold, 1974; Anderson, 1981). Some bushbuck popula-tions show extensive overlap of their home ranges and repeated brief associations among particular females, characteristics suggesting a similar, though still less grega-tious, pattern (Waser, 1974).

Elephants and most hyrax species live in matrilineal groups (Leuthold, 1977; Hoeck, 1982). Interestingly, the more solitary tree hyrax (*Dendrohyrax arboreus*) may have a pro-misian-like social organization (Kingdon, 1971; H. Hoeck, pers. commun.)

Marsupials

While only a few marsupials are gregari-ous, philopatry appears to be widely distrib-uted and occurs in many variant forms. Two species suggest the wide range of undiscover-ed phenomena. Holsworth (1967) reported that only 79 out of 709 marked juvenile quokka moved from their natal territories, though he did not indicate the sexes of those that stayed nor the details of any individual's movements. Philopatry is less ubiquitous in brush-tailed possums, but the data are more complete. Dunnett (1964) found that 4 out

of 6 females followed through their first year bred on their mothers' ranges (their mothers were still alive and reproducing); one male also matured on his father's home range and may have bred there. R. How (1978, pers. commun.) also found both males and fe-males maturing (and females breeding) on their natal home ranges, although the pro-portion of philopatric young in his study was smaller.

Rodents

Lifelong natal philopatry by at least some females is a ubiquitous phenomenon in *Spermophilus* ground squirrels as well as their more gregarious relatives, the prairie dogs and marmots (Table 1). Data on philopatry in woodchucks would be highly desirable; al-though most authors (Grizzell, 1955; Snyder and Christian, 1960; Barash, 1974) have stated that juveniles disperse in their first year of life, Merriam (1971) observed that woodchuck burrows were grouped into "wards" similar to those of prairie dog colonies.

A less well-known continuum occurs among the African mole-rats. This situation is particularly interesting given the existence of the "eusocial" naked mole rat, *Heterocephalus glaber* (Jarvis, 1981). Jarvis (1969, p. 238) has reported that in the blesmol (*Bathyergus suillus*) "small groups probably occupy the same burrow system and form a loose-knit colony." Whether the members of these colonies are related is unknown. But in the root rat, offspring may extend one of the maternal burrows and then close off the pas-sage to the original burrow (Jarvis, 1973). And Jarvis and Sale (1971) have reported that in the silky blesmol three adjacent bur-row systems were all occupied by adults of the same size. They suggested that the three burrow systems were originally part of one system and that their occupants were prob-ably sibs.

Philopatry in Taxa without Gregarious Members

While taxa containing gregarious species include a disproportionate share of solitary species that exhibit prominent philopatry, philopatry also occurs in taxa without grega-rious members. Cricetid rodents and muste-lid carnivores, for instance, both include species in which lifelong philopatry occurs

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re not always suggest similar philopatry in 1982; Owens and colleagues (Ahnlund, et al., 1982), Beechey's and Holdenreid, (1982), Dubost, (1978), (1982), and

acteristics distinguishing them from species without such a bias. In pikas, in which philopatry is temporally male-biased, males and females are both strongly and mutually territorial except when a female is in estrus; the same is true in some red squirrel populations, in which philopatry is female-biased. White-lined bats (male-biased philopatry) practice resource-defense polygyny, as do yellow-bellied marmots (female-biased philopatry).

Nevertheless, the existing evidence does not contradict Greenwood's more general suggestion that sex biases in philopatry are somehow correlated with aspects of the mating system. For instance, Rogers (1977) has suggested that parents tolerate non-dispersal in the sex whose reproductive success they can thereby increase the most. According to Rogers, black bear mothers cannot "aid" their sons, since males require a huge area to find and inseminate multiple females. In contrast, their tolerance of philopatric daughters results in the more rapid growth and earlier sexual maturity of those daughters. Another possibility is that the direction of sex biases in philopatry is correlated with the extent to which an offspring of each sex is a threat to the reproductive success of its same-sexed parent, a situation which in turn would reflect patterns of maternal versus paternal care.

THE TYPES OF NATAL PHILOPATRY

Natal philopatry occurs in three major variants (Table 2):

(1) Parents may tolerate offspring within their home ranges into adulthood, foraging independently and interacting only occasionally. In such cases, the home ranges of parents and offspring extensively overlap, though either offspring or parent may eventually expand its range beyond the original common area. In extreme cases, the home ranges of parents and independent offspring may be virtually congruent; individuals inhabiting "stacked" home ranges have been referred to as members of a "clan" (e.g., Kruuk, 1978a).

(2) Parents may relinquish a part of their home ranges to the offspring, which then tend to be distributed in territories on the periphery of their parents'. The boundaries

between areas used by parents and by offspring may then be maintained by mutual avoidance. Again, the offspring often eventually expand their home ranges beyond this nucleus into areas not originally used by the parent.

(3) Parents may disperse, and thereby relinquish the use of their original home ranges to their offspring.

Home-range sharing (alternative 1), the only form of philopatry compatible with gregariousness, is also by far the most common form among solitary species (see Table 2).

Natural selection might favor either alternative (1) or (2) depending on the spatial distribution of resources, along the lines predicted by many models of animal spacing. Some red squirrels, black bears, and rufous elephant shrews might indeed inhabit spatially homogeneous habitats, subdivisible so that any subset of the mother's total home range would contain a complete range of critical resources. Under these circumstances, offspring could survive in a peripheral subset of the maternal range and (as was first argued by Smith, 1968) nonoverlapping areas of activity might minimize the energetic costs of foraging. But spatial heterogeneity in resource distribution seems likely to be a quite general phenomenon. Wherever resources are not evenly distributed, and particularly where resource locations "move" in space, overlapping home ranges should be favored (e.g., Waser and Wiley, 1979). Several species (red squirrels, black bears) that show interpopulational variation in the likelihood of alternatives (1) and (2) provide a potential test for this hypothesis.

There may be ways in which the cost to a parent of sharing a home range could be reduced. In addition to cooperating with or reproductively suppressing their offspring (see p. 380), females might expand their home ranges beyond their own survival needs and allow their offspring to occupy this excess area. This pattern occurs in a number of species, including round-tailed ground squirrels (Dunford, 1977b), Richardson's ground squirrels (Michener, 1979), European rabbits (Mykytowycz, 1960), and red squirrels (Smith, 1968). Among banner-tailed kangaroo rats, females usually acquire

Form:

Species
Marsupialia
<i>Trichosurus vulpecula</i>
<i>T. caninus</i>
<i>Cynobelideus leadii</i>
Chiroptera
<i>Saccopteryx bilineata</i>
Primates
<i>Calago crassicaudata</i>
<i>C. demidovii</i>
<i>C. senegalensis</i>
<i>Perodicticus potto</i>
Lagomorpha
<i>Ochotona princeps</i>
<i>Oryctolagus cuniculus</i>
Rodentia
<i>Spermophilus richardsoni</i>
<i>S. tereticaudus</i>
<i>S. beldingii</i>
<i>S. beecheyi</i>
<i>S. tridecemlineatus</i>
<i>Tamias striatus</i>
<i>Sciurus carolinensis</i>
<i>Tamiasciurus hudsonicus</i>
<i>Dipodomys merriami</i>
<i>D. spectabilis</i>
<i>Castor canadensis</i>
<i>Peromyscus maniculatus</i>
<i>Microtus arvalis</i>
<i>M. montanus</i>
<i>M. ochrogaster</i>
<i>Arvicola terrestris</i>
<i>Neotoma fuscipes</i>
<i>Mus musculus</i>
<i>Dasyprocta punctata</i>
<i>Microcavia australis</i>
Carnivora
<i>Vulpes vulpes</i>
<i>Ursus americanus</i>
<i>Mustela erminea</i>
<i>Nandina binotata</i>
<i>Hyena brunnea</i>
<i>Felis domesticus</i>
<i>Acinonyx jubatus</i>
<i>Panthera tigris</i>

Artiodactyla

Cephalophus monticola

Includes species in which the parent's next breeding season to breed on the same site. O: parent overlap; P: offspring overlap; E: parents emigrate, offspring.

nearby mounds as thus expand their territory (Jones, unpublished). Females must live long enough time sufficient to so, it is mainly the older and more d afford philopatry. the highest quality therefore best able offspring (Mykytowycz, 1960). Alternative (3): ment of the home

TABLE 3
Life history correlates of natal philopatry¹

Species	No. of litters per year ²	Litter size ³	Annual survivorship ⁴		References
			juvenile	adult	
Marsupialia					
<u>Trichosurus vulpecula</u>	1-2	1	.90	.20-.30	How, 1978; Smith, Brown, and Frith, 1969
<u>T. caninus</u>	1	1	.44	.85	How, 1976, 1978, 1981
<u>Gymnobelideus leadbeateri</u>	1-3	(1-2)			Smith, 1980
Chiroptera					
<u>Saccopteryx bilineata</u>	1	1		.78	Bradbury and Vehrencamp, 1976, 1977
Primates					
<u>Galago crassicaudatus</u>	1	(1-3)	.84	>.85	Charles-Dominique and Bearder, 1979; Clark, 1978
<u>G. demidovii</u>	1	(1-2)		.70	Charles-Dominique, 1972, 1977a
<u>G. senegalensis</u>	1-2	(1-2)			Bearder and Doyle, 1974; Charles-Dominique and Bearder, 1979
<u>Periodictus potto</u>	1	1		high	Charles-Dominique, 1974
Lagomorpha					
<u>Ochotona princeps</u>	1-2	3		.55-.67	Smith and Ivins, in press
<u>Orvetolagus cuniculus</u>	1-7	3.9	.10		Mykutowycz, 1959, 1960; Southern, 1940
Rodentia					
<u>Spermophilus richardsoni</u>	1	4.9-8	.27	.55	Michener, 1979, 1980; Michener and Michener, 1977; Nellis, 1969
<u>S. tereticaudus</u>	1	6.2			Dunford, 1977a; Neal, 1964
<u>S. beldingi</u>	1	5.6	.07-.46	.32-.77	Morton and Gallup, 1975; Sherman, 1981; Turner, 1972
<u>S. beecheyi</u>	1	6.3	.31	.31	Evans and Holdenreid, 1943
<u>S. tridecemlineatus</u>	1-2	6.7	.15-.24	.35-.59	Evans, 1951; McCarley, 1966; Rongstad, 1965
<u>Tamias striatus</u>	1-2	4	.35	.56	Elliott, 1978; Yerger, 1955
<u>Sciurus carolinensis</u>	2	3.1	.40	.46	Thompson, 1978a, b
<u>Tamiasciurus hudsonicus</u>	< 1-2	4.0-4.5			Layne, 1954; Rusch and Reeder, 1978
<u>Dipodomys merriami</u>	2.4	2	.28	.17	Jones, 1982
<u>D. spectabilis</u>	1-2	2	.52	.44	Jones, 1982
<u>Castor canadensis</u>	1	4		high	Bradtr, 1938; Novakowski, 1967
<u>Peromyscus maniculatus</u>	2-3	3.6	.01	.01	Howard, 1949
<u>Microtus arvalis</u>	multiple	7	low	low	Frank, 1954, 1957
<u>M. montanus</u>	multiple	2.5	low	low	Jannett, 1978, 1980
<u>M. ochrogaster</u>	multiple	1-6	low	low	Getz and Carter, 1980; L. Getz, pers. commun.
<u>Arvicola terrestris</u>			low	low	Leuze, 1976
<u>Neotoma fuscipes</u>	1-5	2.2	.33	.32	Linsdale and Tevis, 1951
<u>Mus musculus</u>	multiple	3.7-7.4	low	0	Berry, 1968; Bronson, 1979; Newsome, 1969; Smith, 1954
<u>Dasvoecia punctata</u>	1	1-2	.30	low	Smythe, 1978
<u>Microcavia australis</u>	2-4	2.8	low	low	Rood, 1970
Carnivora					
<u>Vulpes vulpes</u>	1	4-7.1	.35	.70	Ables, 1975; Lloyd, 1980; Storm, 1972
<u>Ursus americanus</u>	< 1	1.6-2.3	.74	.85-.88	Herrero, 1978; Jonkel and Cowan, 1971; Kemp, 1972
<u>Mustela erminea</u>	1	(1-4)		low	J. Erlinge, pers. commun.; Simms, 1979
<u>Nandinia binotata</u>	1	(1-2)			Charles-Dominique, 1978
<u>Hyena brunnea</u>	1	(1-4)		high	Asdell, 1964; Ewer, 1973
<u>Felis domesticus</u>	1-2	3.9		.65	Asdell, 1964; Landré, 1977
<u>Acinonyx jubatus</u>	< 1-2	3		high	Frame and Frame, 1977, 1981
<u>Panthera tigris</u>	< 1	2	.5-.7	high	Schaller, 1967; Snaquist, 1981

Species
Artiodactyla
Cephalophus monticola

Notes:
This and subsequent episode is common while the parent
Ranges
Means or ranges of are given in parentheses
Ranges are given in the order of values are not reported

following the rule disperse to the nearest would have a significant continuing to use all and thus, by our criteria, patric.

In the second case the black bear, the survivorship, in which spring become their on the same or adult will discuss these two

Opportunistic

In a prescient paper (1977) argued that "if near their birth place maturity, [that] a breeding sites, and ant opponents by maximize their] c Assuming further (parents) are always sents and that trans as far as the nearest demonstrated that of juvenile disperse matched that which small vertebrates. Not yet to be tested with life history data and field populations, species will certainly if the opportunity is not need to contest it parent.

Opportunistic philopatric

TABLE 3 (Continued)
Life history correlates of natal philopatry¹

Species	No. of litters per year ²	Litter size ³	Annual survivorship ⁴		References
			juvenile	adult	
<i>Perodactylus</i>	1	1	.70	.90	Dubost, 1980
<i>Phalopus monticola</i>					

¹This and subsequent tables include all species in which philopatry beyond the next parental breeding episode is common in at least one sex, or in which offspring are known to breed in the natal area while the parent remains alive.

²Means or ranges of means where results of several studies differ; if means are unavailable, ranges are given in parentheses.

³Means are given where interpopulation variability is reported. "High" means that adult longevity is in the order of a decade or longer; "low," that adult longevity is rarely greater than one year. If values are not reported by authors, they are estimated from reported mark-recapture data.

Following the rule, "On reaching adult size disperse to the nearest empty home range," would have a significant probability of continuing to use all or part of its natal range and thus, by our definition, would be philopatric.

In the second category are species, such as the black bear, that have a high adult survivorship, in which case philopatric offspring become their parents' contemporaries in the same or adjacent home ranges. We will discuss these two categories separately.

Opportunistic Philopatry

In a prescient paper, Murray (1967, p. 57) argued that "individuals that . . . stay near their birth place until they approach maturity, [that] aggressively compete for breeding sites, and [that] respond to dominant opponents by moving away [would maximize their] chance of reproducing." Assuming further that residents (including parents) are always dominant over transients and that transients would move only as far as the nearest empty site, Murray demonstrated that the expected distribution of juvenile dispersal distances roughly matched that which had been observed in small vertebrates. Murray's arguments have not been tested quantitatively while using life history data and dispersal distances from field populations, but juveniles in many species will certainly settle on the natal range if the opportunity arises—that is, if they do not need to contest its use with a same-sexed parent.

Opportunistic philopatry would involve

no range-sharing between parent and offspring and, indeed, no parental investment of any kind. It seems questionable whether there are many species in which philopatry is both common and solely opportunistic. Even species with high adult mortality rates, such as voles, generally produce young that reach maturity so rapidly that parents are still likely to be alive and breeding. No studies have yet collected the detailed demographic data necessary to recognize philopatry occurring more frequently than expected given the probability of chance openings.

Nevertheless, opportunistic philopatry may have important consequences for the evolution of philopatry in general. Opportunities for inheriting the parental home range may not be the norm for many species, but they are at least occasional for all. The advantages to a maturing juvenile of preferring philopatry are quite general: non-dispersing animals have a built-in familiarity with the dangers and resources of their home ranges, they run none of the risks of dispersing, and the vicinity of the natal range is arguably the area where suitable habitat and mates are most likely to be found (cf., Howard, 1960; Lidicker, 1975; Anderson, 1980; Gaines and McClenaghan, 1980; Shields, 1982). Selection would then be expected to favor the spread of a tendency toward opportunistic philopatry if it arose in any mammalian population, even if it were not the ancestral state. Once established, it is easy to imagine the modification of thresholds for philopatry, so as to result in increas-

ingly delayed dispersal or in higher probabilities of nondispersal even when parents remain alive. For instance, the fall generation of juveniles in prairie deer mice (King, 1963), house mice (Anderson, 1970), and several vole species practice opportunistic philopatry. Adults rarely survive the winter, and philopatric fall juveniles inherit the parental nest and home range. In some species, philopatric tendencies characterize some members of spring generations as well—either by early litters remaining with the mother (prairie voles: Getz and Carter, 1980) or by parental emigration when the offspring reach adulthood (some montane voles: Jannett, 1978).

Philopatry by Parental Consent

Many of the species in which philopatry has been noted as being common share relatively high adult survivorship rates and low rates of reproduction (see Table 3). It is in these species that the interests of parents and offspring may differ, for competition with philopatric offspring may decrease the parents' future reproductive rate. Yet there is no obvious lack of philopatric tendencies in species with high adult survivorship. Philopatry is as common in species with high annual survivorship rates as it is in shorter-lived species (12 out of 33 species in Table 3 have annual survivorship rates above 0.67, compared to 13 out of 33 below 0.33 and only 8 out of 33 with intermediate annual survivorship.)

In some taxa (notably canids, galagos, and heteromyid rodents), there is a trend in the direction opposite from that expected if philopatry were opportunistic: species with lower adult mortality rates show more frequent or extensive natal philopatry. A related trend occurs in terrestrial sciurids. Armitage (1981) found that age of dispersal in this group increases with adult body weight. Do species with greater adult body weight also tend to be longer-lived? If so, sciurids show the same perverse trend, namely, parents are more likely to tolerate nondispersing offspring when, as a result of high parental survivorship, they would seem more likely to have to pay a cost in reduced future reproduction.

Ecological Correlates of Natal Philopatry

Correlation of prolonged natal philopatry with high adult survivorship would make sense if parents tolerate their nondispersing offspring wherever opportunities for successful dispersal are rare—the "habitat saturation" hypothesis. We can examine this and other hypotheses advanced in the literature by comparing the ecological characteristics of philopatric species (Table 4).

Habitat Saturation

Smith (1978) studied pika populations in Alberta, Colorado, and California. The populations differed in degree and constancy of habitat saturation, defined as the proportion of usable talus patches occupied by pikas. Smith was able to correlate demographic characteristics with these variables. Yet, despite the advocacy of habitat saturation as a determinant of natal philopatry in communally breeding birds (Brown, 1974, 1978; Gaston, 1978; Stacey, 1979; Trail, 1980; Koenig and Pitelka, 1981; Emlen, 1982), no studies of mammals have directly investigated the effects of saturation on the proportion of philopatric offspring.

If habitat saturation were the primary ecological condition that favors natal philopatry, only opportunistic philopatry would be expected in populations subject to density-independent regulation. Populations that are usually below carrying capacity for other reasons would also be of interest—for instance, those populations limited by predation or disease, or subject to drastic changes in carrying capacity between breeding seasons. Into such categories might fall the gray fox and striped skunk, which in some areas are regulated by disease (Trapp and Hallberg, 1975; Verts, 1967), and the Virginia opossum, which in much of its range is limited by predators or winter climate (Fitch and Sandidge, 1953; Llewellyn and Dale, 1964). Philopatry is not extensive in these species (see Table 1). More generally, the resources inferred to limit population sizes in species commonly regarded as philopatric are (1) food and (2) den sites, both of which are presumably density-dependent (see Table 4).

Species	
Marsupialia	
	<u>Trichosurus vul</u>
	<u>T. caninus</u>
	<u>Gymnobelideus l</u>
Chiroptera	
	<u>Saccopteryx bil</u>
Primates	
	<u>Galago crassica</u>
	<u>G. demidovii</u>
	<u>G. senegalensis</u>
	<u>Periodictus pot</u>
Lagomorpha	
	<u>Ochotona prince</u>
	<u>Oryctolagus cun</u>
Rodentia	
	<u>Spermophilus ri</u>
	<u>S. tereticaudus</u>
	<u>S. beldingi</u>
	<u>S. beecheyi</u>
	<u>S. tridecemline</u>
	<u>Tamias striatus</u>
	<u>Sciurus carolin</u>
	<u>Tamiasciurus hu</u>
	<u>Dipodomys merri</u>
	<u>D. spectabilis</u>
	<u>Castor canadens</u>
	<u>Peromyscus mani</u>
	<u>Microtus arvali</u>
	<u>M. montanus</u>
	<u>M. ochrogaster</u>
	<u>Arvicola terres</u>
	<u>Neotoma fuscipe</u>
	<u>Mus musculus</u>
	<u>Dasyprocta punc</u>
	<u>Microcavia aust</u>
Carnivora	
	<u>Vulpes vulpes</u>
	<u>Ursus americanus</u>

TABLE 4
Ecological correlates of natal philopatry

Species	Food Type ¹	Potential Limiting Factors ² Den/Nest Sites	Food	Comments ³	References
<i>Peromyscus</i>					
<i>Peromyscus</i>	V	yes	yes	PH	Dunnnett, 1964; How, 1978
<i>Peromyscus</i>	V	yes			How, 1978
<i>Peromyscus</i>	I, G	no	yes		Smith, 1980
<i>Peromyscus</i>					
<i>Peromyscus</i>	I	no	yes	PF	Bradbury and Vehrencamp, 1976
<i>Peromyscus</i>					
<i>Peromyscus</i>	G, I, F	no	yes	PH, PF	Clark, 1978
<i>Peromyscus</i>	I, F	no			Charles-Dominique, 1977a
<i>Peromyscus</i>	I, G	no		PH	Charles-Dominique and Bearder, 1979
<i>Peromyscus</i>	G, F, I	no	yes		Charles-Dominique, 1974
<i>Peromyscus</i>					
<i>Peromyscus</i>	V			PH, C	Smith, 1978
<i>Peromyscus</i>	V	yes	yes	C	Nykytowycz, 1959, 1960; Southern, 1940
<i>Peromyscus</i>					
<i>Peromyscus</i>	V	yes			Yeaton, 1972; Michener, 1973, 1979
<i>Peromyscus</i>	V, S, F, I	yes			Morton, 1975; Turner, 1972
<i>Peromyscus</i>	V, F, I	yes		D, L	Evans and Holdenreid, 1943; Linsdale, 1946
<i>Peromyscus</i>	V, I	yes			Evans, 1951; Rongstad, 1964
<i>Peromyscus</i>	F, I	yes		C	Elliott, 1978; Yerger, 1955
<i>Peromyscus</i>	F		yes	PF, C, L	Flyger, 1960; Thompson, 1978b
<i>Peromyscus</i>	F, V, I	no	yes	C	Layne, 1954; Rusch and Reeder, 1978; Smith, 1958
<i>Peromyscus</i>	S	no	yes	C	Reynolds, 1960
<i>Peromyscus</i>	S	yes	yes	C, D	Vorhies and Taylor, 1922
<i>Peromyscus</i>	V	yes	yes	PH, C, D	Bradt, 1938
<i>Peromyscus</i>	F, I	no		C	Howard, 1949
<i>Peromyscus</i>	V	no	yes	C	Frank, 1957
<i>Peromyscus</i>					
<i>Peromyscus</i>	V			PH	Getz and Carter, 1980
<i>Peromyscus</i>	V		yes	C, L	Airolidi, 1978; Leuze, 1976
<i>Peromyscus</i>	V, F	yes		C, D	Cranford, 1977; Linsdale and Tevis, 1951
<i>Peromyscus</i>	S, I, V, F			L	Whitaker, 1966; Young et al., 1950
<i>Peromyscus</i>	F	no	yes	L	Galef and Clark, 1976; Smythe, 1978
<i>Peromyscus</i>	V				Rood, 1970
<i>Peromyscus</i>					
<i>Peromyscus</i>	C, I, F	yes	yes	PF	Ables, 1975; Follman, 1973; MacDonald, 1981
<i>Peromyscus</i>	C, I, F	yes	yes	PF	Jonkel and Cowan, 1971; Rogers, 1977

TABLE 4 (Continued)
Ecological correlates of natal philopatry

Species	Food Type ¹	Potential Limiting Factors ²			References
		Den/Nest Sites	Food	Comments ³	
<i>Mustela erminea</i>	C		yes	PH	Erlinge, 1977
<i>Nandinia binotata</i>	F, I	no		PF	Charles-Dominique, 1978
<i>Hyaena brunnea</i>	C	yes	yes	PF	Mills, 1982; Owens and Owens, 1978
<i>Felis domesticus</i>	C, I	yes	yes	PF	Liberg, 1980
<i>Acinonyx jubatus</i>	C	no	yes	L	Frame and Frame, 1981
<i>Panthera tigris</i>	C		yes	L	Schaller, 1967; Sunquist, 1981
<i>Artiodactyla</i>					
<i>Cephalophus monticola</i>	F	no	yes	PF	Dubost, 1980

Notes:

¹C = vertebrate prey, including carrion; I = invertebrates; F = fruit, nuts, fungi; S = seeds; V = vegetation, including grass, leaves, bark; G = plant gums. Items are listed in order of decreasing importance, with rare items excluded.

²Factors suggested as limiting by the authors cited. No limiting factors other than these two are suggested for these species.

³Comments: other factors that may favor philopatry; PF = food distribution is patchy; PH = habitat distribution is patchy; C = adults construct large food caches important to survival; D = adults construct large houses, dens, or other "improvements" important to survival; L = learning home range attributes (where to hunt, what to eat, where safe sites are) may be important to survival.

If population density per se reflects habitat saturation, then the results of several studies of microtine rodents are consistent with this hypothesis. Many such studies have found the highest dispersal rates occurring while cycling populations are increasing in size ("presaturation" dispersal), whereas at peak densities there seem to be fewer dispersers (e.g., Krebs et al., 1976; Stenseth, in press). Another common trend is for the lowest dispersal tendency to be found in females of autumn litters, when population density is highest, and for dispersal tendencies to increase after a winter die-off (e.g., Frank, 1957; Myllymäki, 1977a, b). While these studies do not directly document natal philopatry, conditions under which dispersal from local populations is less successful are presumably also those under which dispersal from the natal area should become less favored. In a related observation, Jannett (1978) discovered that montane vole females abandoned their nests and home ranges to their young at low population densities, whereas at higher densities the females remained with their litters to form extended maternal families.

Like "habit saturation," the absence of

empty or marginal habitats ("dispersal sinks") should decrease the chances of successful dispersal (Lidicker, 1975; cf., Koenig and Pitelka, 1981). Tamarin (1977) compared island and mainland populations of meadow voles and concluded that there was reduced dispersal on islands. Similarly, studies of prairie deer mice have suggested that island residents are poorer dispersers than their mainland counterparts, and that this is a result of selection against dispersers under the highly competitive conditions on islands (Redfield, 1976; Sullivan, 1977).

In cycling populations of Swedish red foxes, Lindstrom and others (Lindstrom, 1982; von Schantz, 1981a, b) have found that territory size is adjusted to support a pair during years of lowest vole abundance, and that this size remains similar during peak density years. In years of increasing density, daughters remain within their parents' territories, which now contain enough food to sustain both daughter and continued parental reproduction. Daughters disperse during years of declining vole abundance. These results suggest an important complication affecting inferences about philopatry and habitat saturation: by main-

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maintaining a constant territory size, foxes behaviorally maintain a constant habitat saturation in the face of large changes in prey density. The probability of philopatry still tracks prey levels, but the mechanism is that philopatric tendencies increase as food within a territory increases and thus becomes more "sharable."

Risky Dispersal and Sharable Resources

Many authors have speculated that spatial patchiness in resources is related to philopatry. For instance, philopatry might be favored if areas of suitable habitat are themselves widely separated by areas that are unsuitable for settlement, yet hazardous to cross. Patchy distributions of critical habitat have indeed been noted for a number of species showing philopatry (see Table 4).

On another scale, resource clumping might also favor natal philopatry; this may occur where resources occur in patches that a few individuals can monopolize. Monopolization of resource patches should have two effects related to philopatry. By decreasing dispersers' access to important resources, it would decrease the likelihood of successful dispersal. Secondly, if monopolized patches contain more food than one individual can exploit, then females holding them can share resources with offspring at no great cost to themselves. Clark (1978) has suggested the existence of such a link between natal philopatry in some populations of thick-tailed bushbabies and their dependence for reproduction on isolated clumps of suitable food-producing trees. Among kit foxes (Goughly, 1981) and white-tailed mongooses (Waser, unpub.), increased philopatry can be inferred in areas richer in suitable sites for breeding dens.

Clumped resources may be sharable even if they are not fixed in space (e.g., Kruuk, 1978b). Into this category might fall fruiting trees for palm civets and duikers, carion for brown hyaenas, and earthworm patches for European badgers and some red foxes. As a consequence of the reduced cost of home range sharing, philopatry—especially philopatry by parental consent—might arise more easily in populations that are using patchy food sources. Among long-lived spe-

cies, most examples of natal philopatry occur in frugivores or carnivores, whose food types are often regarded as patchy in distribution. Relatively few cases of philopatry occur in grazers or folivores (for example, only 2 out of 15 species with adult survivorship >0.67 ; see Tables 3, 4).

Rapid food renewal rates may also make resources sharable (Waser, 1981), and thus increase the likelihood of philopatry in insectivorous and gum-feeding species (see Table 4).

Other Ecological Factors

Some authors have suggested that natal philopatry would be favored where familiarity with foraging areas is crucial. Young black bears, for example must be able to find widely scattered, evanescent fruit crops (Rogers, 1977), and young two-toed sloths must learn the locations of individual trees the leaves of which they are equipped to detoxify and digest (Montgomery and Sunquist, 1978). Similar arguments have been advanced where offspring significantly increase their survivorship by learning other attributes of their natal range, such as the locations of travel routes or runways (elephant shrews, bannertailed kangaroo rats, Beechey ground squirrels, grey squirrels, house mice) or of sites safe from predators (muntjacs, agoutis) (see Table 4). Finally, philopatry might be more likely in species in which females must make large investments in their home ranges before reproduction is possible. Examples often cited are the houses of woodrats and the dens and food caches of beavers. When burrows require considerable time and effort to construct, the acquisition of an existing burrow may be an essential prerequisite for survival and reproduction. If survival to reproductive age requires access to such a burrow—or similarly, to a substantial food cache or any other home range improvement—opportunities for dispersal will be effectively restricted (see Table 4). This is the case for bannertailed kangaroo rats, which live in large mounds that require months to construct and may contain up to six kilograms of stored seed. New mounds are rarely built; instead, existing mounds are passed on from individual to individual within a population. Often juve-

nile bannertails inherit a mound from their mothers (Jones, 1982).

CONSEQUENCES OF NATAL PHILOPATRY

Neighboring Adults Include Close Kin

The most obvious and widespread consequence of natal philopatry is an increased likelihood that close kin are clustered as adults (Table 5). But the taxonomic distribution of natal philopatry is not congruent with the distribution of kin clustering for two reasons. As noted earlier, survivorship or fecundity schedules may ensure that even where natal philopatry occurs, few philopatric individuals have surviving kin nearby by the time they mature. On the other hand, kin may be neighbors in the absence of natal philopatry if openings in adjacent home ranges are frequent enough that dispersers need move only to the immediately adjacent area. For instance, kin adjacency without philopatry has been reported in gray foxes (Foliman, 1973), elephant shrews (Rathbun, 1979), and in some mustelids (Gerell, 1970; Erlinge, 1977; Simms, 1979).

In species within which natal philopatry has been commonly observed, the most widespread form of relatedness among adult neighbors is that of mother and daughter (31 out of 39 species; see Table 5). Female sibs remain immediate neighbors as adults in somewhat fewer species (20 out of 39). Other combinations of parent with grown offspring or of grown sibs are neighbors less frequently.

Two processes probably contribute to the rarity of reported adult kin associations other than mother-daughter and sister-sister. The frequency of kin associations involving males is undoubtedly reduced by their generally lower probabilities of philopatry. As would be expected, most of the 15 cases of kin adjacency involving sons (see Table 5) are found either in species with male-biased philopatry or in small mammals with significant philopatry in both sexes. In bannertailed kangaroo rats, we have observed at least seven instances in which a mother and son both survived to breed in adjacent ranges. Howard (1949) found several examples of mother-son and daughter-son adjacency in prairie deer mice (see below).

In addition, kin associations involving males may be underreported as a result of difficulties in assessing paternity. For instance, where males are sedentary as adults and long-lived, nondispersing daughters would often mature within or adjacent to their fathers' home ranges. Species with long-term pair bonds demonstrate that fathers and adult daughters are not infrequently neighbors. Female rufous elephant shrews that disperse to neighboring home ranges remain adjacent to their fathers as adults (Rathbun, 1979). Canids, among which both long-term monogamy and female philopatry are widespread, have the potential to provide further examples. As noted earlier, where several fox females share breeding dens, "young" and "old" adults are often reported to be involved. The tenure of an average male in a pair is sufficiently long that a significant proportion of these cases could involve father, mother, and daughter.

These examples raise the question, Do the adverse effects of inbreeding universally produce individuals that avoid philopatry in the presence of opposite-sexed kin? In some instances, adult movements do seem specifically linked to inbreeding avoidance: adult male Belding's ground squirrels are reported to move coincidentally with the maturation of their probable daughters, with the most highly polygynous males moving the farthest (Sherman, 1981). But some close inbreeding certainly occurs in natural populations. A well-documented case is that of prairie deer mice, in which Howard (1949) found 10 presumed cases and 7 other possible cases of close inbreeding in a two-year study. Of these 17 instances, 10 involved father-daughter matings, 2 involved mothers and sons, and 5 were between siblings. These matings produced at least 4 per cent of the litters he observed during the study, yet 69 per cent ($n = 77$) of the males and 85 per cent ($n = 78$) of the females remained within 500 feet of their birthplaces throughout their lives. In other species, anecdotal reports of close inbreeding are not uncommon. For instance, A. Smith (pers. commun.) has reported a case of a male pika dispersing to a territory adjacent to his mother's, and then breeding with her. Hendrichs (1975) sus-

Species
Arthropoda
<i>Trichosurus vulpe</i>
<i>T. caninus</i>
<i>Yanobelideus lea</i>
Chiroptera
<i>Saccopteryx biline</i>
Primates
<i>Alago crassicaud</i>
<i>A. demidovii</i>
<i>A. senegalensis</i>
<i>Perodicticus potto</i>
Morphia
<i>Photona princeps</i>
<i>Cryptolagus cunicu</i>
Sciuridae
<i>Peromophilus richa</i>
<i>A. terebricaudus</i>
<i>A. beldingi</i>
<i>A. beecheyi</i>
<i>A. tridecemlineatus</i>
<i>Tamias striatus</i>
<i>Tamias carolinensis</i>
<i>Tamiasciurus ludson</i>
<i>Perodromus merriami</i>
<i>A. spectabilis</i>
<i>Sciurus canadensis</i>
<i>Peromyscus manicula</i>
<i>Peromyscus arvalis</i>
<i>A. montanus</i>
<i>A. ochrogaster</i>
<i>Sciurus terrestris</i>
<i>Sciurus fusciceps</i>
<i>A. musculus</i>
<i>Peromyscus punctata</i>
<i>Peromyscus australis</i>
Canidae
<i>Canis vulpes</i>
<i>C. americanus</i>
<i>Canis erminea</i>
<i>Canis pinotera</i>
<i>Canis brunnea</i>
<i>Canis domesticus</i>
<i>Canis tubatus</i>
<i>Canis tigris</i>
Urocyon
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Urocyon
1M: mother, D:
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TABLE 5

1M: mother, D: daughter, F: father, S: son; references as in Table 1.
²X: home range overlap among adult members of philopatric sex (or among adult kin) is greater than that among members of the dispersing sex (or among adult nonkin), C: clan or communal home ranges; multiple adults forage independently within a common home range, little or no overlap between neighboring clan home ranges
³B: close adult kin respect mutual home range boundaries without aggression, T: levels of aggression between close adult kin in encounters are lower than among adult nonkin irrespective of the location of the encounter, D: close adult kin share a den or nest, R: adults share common hunting trails or runways

pected two of the dikdik pairs he observed to consist of mothers and sons. Harris (1980) has reported a mated brother-sister red fox pair. MacKinnon and MacKinnon (1981) inferred father-daughter breeding in spectral tarsiers. To what extent does breeding with close relatives actually depress reproductive success? And if it does depress success, do heterosexual kin associations occur less frequently than expected by chance, given the two sexes' independent probabilities of philopatry and survival?

Increased Tolerance among Related Neighbors

A common, but not universal, correlate of philopatry is an increased home-range overlap (HRO) in the nondispersing sex relative to the dispersing one (see Table 5). An increased HRO seems an intuitively reasonable consequence of natal philopatry if philopatric adults have kin as neighbors and if kinship decreases the cost of mutual tolerance (note, however, that HRO is not a necessary correlate of philopatry, as demonstrated, for instance, by black bears).

In some species, data are adequate to demonstrate greater home-range overlap among female kin than among female nonkin. For instance, muntjac females living in large enclosures have home ranges overlapping 70 per cent with those of sexually mature daughters, but only 10 per cent with female nonkin (Dubost, 1970). A similar situation occurs in Richardson's ground squirrel (Michener and Michener, 1977; Michener, 1979). In extreme cases, female relatives may occupy virtually congruent home ranges that do not overlap with those of neighboring but unrelated females. Within matrilineal, feral housecats in Sweden had home ranges that "overlapped almost exclusively, especially over a long period . . . [though] within the communal home range, the individuals might have different favorite areas" (Liberg, 1980, p. 341). Between matrilineal, Liberg observed little or no home-range overlap.

Among housecats and muntjacs, increased home-range overlap is known to reflect not only a tendency for daughters to center their activities nearer mothers than other females, but also increased tolerance (i.e., decreased probabilities of aggression upon encounter).

Decreased aggression within as compared to between matrilineal is implied in many behavioral phenomena, including nestsharing and use of joint runways (see Table 5). Decreased aggression between mothers and daughters or between sisters compared to less closely related females has been particularly well documented among round-tailed ground squirrels (Dunford, 1977b), Richardson's ground squirrels (Michener, 1973), and Belding's ground squirrels (Sherman, 1980).

Although cases of extensive home-range overlap usually involve close kin, there are exceptions. Fritzell (1978) reported a case of near-total HRO between two same-aged female raccoons known not to be sisters. Owens and Owens (1979) reported that brown hyaenas within a clan are not necessarily close kin. Apparently unrelated male palm civets may share nearly identical territory boundaries (Charles-Dominique, 1978). Female spear-nose bats that share a roost and overlapping home ranges are a genetic random sample of the local population (McCracken and Bradbury, 1981).

It would appear that female nondispersal could be rejected as a concomitant of female home-range overlap in such cases, but two qualifications are necessary. First, "mistakes" such as tolerating an occasional unrelated female when most neighbors are close kin can be eliminated by natural selection only if means of recognizing those mistakes as such are available. Such mistakes ought to be less common, therefore, wherever indications of kinship are prominent and where those cues occur frequently (i.e., where life-history and dispersal characteristics are such that the kin categories to be distinguished are often neighbors). Second, even in the absence of any ability to recognize one's kin, natural selection can favor increased tolerance of a class of individuals if the probability of its members being close kin is high enough. This point has been neatly demonstrated by Seger (1976), who worked on a parallel problem in plants. Using simulation techniques, Seger established that genetically leading organisms to devote less energy to interference competition (overshadowing competitors) and more to reproduction (seeds) could spread when interactions were

kin-biased. The critically dependent distance (of a determined the proportion that would

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tion that would involve kin.

In any case, data on home-range overlap
and behavioral tolerance indicate that soli-
tary, as well as gregarious mammals, do not
behave equally towards all conspecifics, but
often make distinctions on the basis of re-
latedness. This point has important implica-
tions for the theoretical treatment of mam-
malian spacing systems, since almost without
exception existing discussions of spacing
assume that the costs and benefits of exclud-
ing one neighbor are the same as those ap-
plying to any other (or at least to any same-
sexed adult). Treisman (1977), Grafen
(1979), and Hines and Maynard Smith
(1979) have begun to analyze conflicts
among kin by using game theory models,
not only to the point of confirming the intu-
itive conclusion that stable strategies for con-
flicts among kin should be less destructive
than involve playing "hawk" with a lower
frequency) than for conflicts among non-kin.

Other Consequences for Spacing

In addition to effects on home-range over-
lap, natal philopatry appears to have a num-
ber of further consequences for spacing in
solitary mammals:

(1) Where all individuals, even close kin,
have mutually exclusive home ranges, the
means by which exclusion is maintained
may depend on the relatedness of the inter-
actants. For example, Rogers (1977) has
reported that black bear mothers simply
avoid using sections of their home ranges
occupied by daughters once these progeny
have become independent. The withdrawal
seems altruistic in the sense that the daugh-
ter's area may be superior bear habitat and
initially preferred by the mother, and that
daughters in unshared areas gain weight
faster than those who do share. Observed
mother-daughter contacts remain amicable;
certainly daughters are not in any position to
expel their mothers, who weigh three to five
times as much as they do. In contrast, terri-
tory boundaries with non-kin are determined
by aggressive interactions.

Early observers of mammalian territori-

ality (e.g., Hediger, 1949; Leyhausen, 1965;
Lockie, 1966) pointed out that solitary mam-
mals, unlike birds, were unlikely to be able
to detect and actively exclude all intruders.
Nevertheless, many solitary mammals main-
tain virtually exclusive home ranges. Most
field observers have been left with the im-
pression that boundaries are maintained by
mutual avoidance, or by avoidance of scent
marks, rather than by direct confrontation.
If trespassers are unlikely to be detected,
why should they avoid trespassing? That
avoidance-based spacing mechanisms should
evolve when neighbors are kin is an intrigu-
ing possibility.

(2) When close kin forage alone but in a
common area, it may be of mutual advan-
tage to so pattern foraging as to avoid areas
recently depleted by other individuals.
"Time-plan" spacing, in which individuals
use the same space but not at the same time,
was first described in housecats by Ley-
hausen (1965). Eaton (1970) subsequently
interpreted observations on the use of space
by cheetahs in the same terms. It is sugges-
tive that these two species both illustrate
common nondispersal of daughters. It is
considerably easier to imagine that such a
system would resist invasion by a "cheater" if
neighbors are kin. Unfortunately, no studies
of solitary mammals have explicitly investi-
gated the relative movements of same-sex
individuals whose ranges overlap, though
the techniques for simultaneous radiotrack-
ing and for a suitable analysis of the data
exist (MacDonald, Ball, and Hough, 1980).

(3) When the home ranges of kin overlap,
individuals could benefit mutually by inde-
pendent patrolling or defense of the common
area. Sherman (1980) has reported "co-
defense" of females' burrow vicinities to be
more common by sisters than by cousins or
unrelated female Belding's ground squirrels,
and more common between mother and
daughter than between sisters. European
rabbits, red foxes, and some microtines are
thought independently to defend a common
boundary (Frank, 1957; Mykytowycz, 1959;
MacDonald, 1980a). Though kin relation-
ships were not ascertained by him, Kruuk
(1978a) has reported that all members of a
badger clan independently visited and
marked latrine sites. The same is true for

anal scent marking by brown hyaenas (Owens and Owens, 1978) and white-tailed mongooses (Waser, unpub.). Wherever independently foraging individuals share a communal or clan home range which is distinct from that used by neighbors, the opportunity for joint (though independent) defense exists. Such a pattern is widespread in philopatric species (see Table 5; also quokkas, spectral tarsiers, kit foxes, bush squirrels, and brush-tailed porcupines).

(4) Where natal philopatry is common, dens or home ranges may become clumped around those of founding individuals. Clumped dens occur in the absence of obvious habitat constraints in many species, particularly among terrestrial sciurids (Richardson's, Beechey, and thirteen-lined ground squirrels) and among some microtines (e.g., common voles) and canids (arctic and bat-eared foxes). The resultant clustering of same-sexed individuals, usually females, may then have consequences for the evolution of mating systems by increasing the number of cases in which males can defend "clumps" of females beyond those dictated directly by ecological constraints.

Cooperative or Manipulative Behavior among Neighbors

By confining our review to solitary mammals, we have explicitly excluded the possibility of forms of cooperation requiring continuous close contact. Nevertheless, it is notable that traits otherwise characterizing only highly gregarious species occur occasionally in species that are solitary. Provisioning of young by older sibs has been reported in the red fox, arctic fox (Hersteinsson and MacDonald, 1981), captive bat-eared fox (B. Beck, pers. commun.), brown hyaena (Mills, 1982), and small Indian mongoose (Lloyd-Jones, 1953). Prairie vole offspring sometimes remain in the nest and incubate and retrieve younger sibs, at least in captivity (Getz and Carter, 1980). Thick-tailed bushbabies may leave their offspring with close kin while they themselves forage (Clark, 1978).

Other forms of kin cooperation, such as the joint marking of a common territory or calling in response to predators, do not re-

quire group living. Dunford (1977a), Sherman (1977), and Schwagmeyer (1980) have used the production of alarm calls by female ground squirrels as evidence that such calls are more strongly favored in the philopatric sex. Smith (1978) found no evidence, however, of an effect of female philopatry on the likelihood of alarm-calling by red squirrels. Thus, a correlation between philopatry and alarm-calling remains to be extended to taxa other than ground squirrels.

Parental manipulation of offspring—in particular, reproductive suppression—would seem less likely in solitary than in gregarious species. If it does occur, reproductive suppression might be expected wherever dens or breeding sites are in short supply, so that parents can monopolize them. Indeed, no more than one European badger pair usually breeds per sett (Kruuk, 1978a), nor does more than one vole female breed per nest (Getz and Carter, 1980; Jannett, 1980; Madison, 1980). Reproductive maturity is delayed in philopatric males, relative to dispersing males, in high-density housecat populations (Dards, 1978) and in white-lined bats that remain in natal roosts (Bradbury and Vehrencamp, 1976). Yearling females may show delayed reproduction, and only one female breeds in many red fox families (Macdonald, 1979b; Harris, 1980)—but there are exceptions (e.g., Storm et al., 1976).

In contrast, several philopatric black bear females bred earlier than those that dispersed (L. Rogers, pers. commun.), and philopatric female cheetahs are sexually active from the time of independence (G. Frame, pers. commun.). Data on reproductive timing of philopatric and dispersing females in other species known to breed while their mothers are alive (see Table 1) might illuminate the conditions under which reproductive suppression evolves. Communal suckling—which would seem to be the antithesis of reproductive suppression—has been reported in housecats (Laundré, 1977; MacDonald and Apps, 1978; Liberg, 1980), red foxes (MacDonald, 1979b), bat-eared foxes (Reynolds, 1976), brown hyaenas (Owens and Owens, 1979; Mills, 1982), field mice (King, 1963), house mice

(Sayler and Salmon, Rood, 1970).

CONCLUS

THE ROLE OF PHIL EVOLUTION OF MAMMAL

Natal philopatry occurs in all mammals. Species may or may not be gregarious. Observations delineate a research.

What is the expected relative success for dispersing vs. philopatric juveniles and what are the values of these factors? Remarkable data are available on these issues, but understanding the evolutionary significance of natal philopatry: philopatric red foxes are known to have more success than dispersers (Stearns, 1980); philopatric rabbits grow faster than dispersers (Mykietowycz, 1960; Rogovin, 1978). Studies addressing the evolutionary significance of natal philopatry could profitably investigate not only of habitat saturation but also of other factors that might be expected to influence the merits of natal philopatry. These factors include the quality of home-range quality and resource attributes that might be expected to influence home-range sharing.

The likelihood that philopatry should depend on the extent to which it produces benefits to kin. Yet the average relative benefits of individual with its neighbors, and the particular neighborhood degrees of relatedness, are not calculated for any solitary species. A primary aim of future studies should be to replace the qualitative information available with the quantitative information necessary to calculate such

Sayler and Salmon, 1971), and caviar (Rood, 1970).

CONCLUSIONS:

THE ROLE OF PHILOPATRY IN THE EVOLUTION OF MAMMALIAN SOCIAL SYSTEMS

Natal philopatry occurs in many, but not all, mammals. Species in which it occurs may or may not be gregarious. Each of these observations delineates an avenue for future research.

What is the expected average reproductive success for dispersing, as compared to philopatric, juveniles and for parents tolerating or driving out a maturing offspring and how are these values influenced by ecological factors? Remarkably few data are yet available on these issues, which are central to understanding the conditions under which natural selection should favor philopatry: philopatric red foxes and water voles are known to have much lower mortality rates than dispersers (Storm, 1972; Leuze, 1980); philopatric rabbits and black bears grow faster than dispersing individuals (Mykutowycz, 1960; Rogers, 1977); female brushtailed possums with philopatric daughters lose their next year's young (How, 1978). Studies addressing these questions could profitably investigate the effects not only of habitat saturation and of adult turnover rate but also of other factors likely a priori to influence the merits of dispersal and philopatry. These factors include local variance in home-range quality, dispersal risk, and resource attributes that decrease the cost of home-range sharing.

The likelihood that philopatry leads to gregariousness should depend in part on the extent to which it produces a local clustering of kin. Yet the average relatedness of an individual with its neighbors, or the probabilities that particular neighbors will have particular degrees of relatedness, are as yet uncalculated for any solitary mammal. A primary aim of future studies should be to replace the qualitative information now available with the quantitative data on survivorship, fecundity, and dispersal rates necessary to calculate such probabilities.

Recent research on mammalian social systems has increasingly emphasized phenomena in gregarious species for which natal philopatry is a prerequisite: the cooperative raising of young by close-kin, the reproductive suppression of maturing offspring by their parents, the competition among sibs for opportunities to inherit parental prerogatives, and the cooperative defense of prey or territory. It has not been widely appreciated that natal philopatry itself is a considerably more widespread phenomenon than is gregariousness. Therefore, social factors hypothesized to promote a prolonged association of offspring with parents, like opportunities to feed or guard siblings, cannot alone account for the presence of mammalian philopatry. The widespread occurrence of natal philopatry in solitary members of taxa that also contain gregarious representatives implies that such phenomena as "helping" at the den or cooperative territory defense can be heuristically viewed as arising secondarily, with philopatry a necessary but not sufficient condition. The widespread distribution of natal philopatry in solitary mammals and its potentially central role in the evolution of complex social groups suggests a revised phrasing of the question, How have such complex groups arisen? In our view, this question can usefully be asked in two steps: First, what conditions lead to natal philopatry? And second, where natal philopatry does occur, what conditions favor further cooperation and gregariousness?

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