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A comparative analysis of non-offspring nursing

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Abstract. Information on the incidence of non-offspring nursing in 100 mammalian species was assembled from the literature and from a questionnaire survey. A comparative analysis of these data revealed several factors that influence the occurrence of non-offspring nursing across species. The incidence of non-offspring nursing is increased by captivity. In field studies, it is more common in species that have larger litters and there are several important differences in the context of non-offspring nursing between monotocous taxa (where females typically give birth to a single young) and polytocous taxa (where females routinely give birth to multiple young). In monotocous species, non-offspring nursing is associated with high levels of 'milk theft' by parasitic infants; and is more common in species where females continue nursing after they have lost their own young. In polytocous species, non-offspring nursing is not associated with 'milk theft' and is most common in species that live in small groups. These results are discussed in terms of the costs to females of tolerating non-offspring nursing.

Despite several recent reviews on communal care in mammals (e.g. Hrdy 1976; Riedman 1982; Gittelman 1985), there has not been a systematic investigation into the ecological correlates of communal rearing. This is partly due to the wide variety of phenomena that can be considered to involve communal care. The most extreme manifestation of communal care by female mammals involves nursing the offspring of another female. The transfer of milk to non-offspring has been confirmed by the use of radio-isotopes (Sheridan & Tamarin 1983; Hoogland et al. 1989). In this review, we focus exclusively on non-offspring nursing because it is a well defined behaviour pattern that is likely to confer definite benefits to infants.

Non-offspring nursing is often implicitly assumed to have mutualistic advantages because of increased levels of nutrition for all of the young. The only studies to show such an effect were on laboratory rodents (Sayler & Salmon 1969, 1971; Mennella et al. 1990). Females that nursed additional pups produced greater quantities of milk per pup. However, these were laboratory studies where the females were given unlimited access to food (Sayler & Salmon 1969; Mennella et al. 1990). In naturalistic conditions, milk would be a limited resource that would have to be distributed with care. By nursing additional offspring, a mother either reduces the amount of nutrients available to her own young or increases the amount of time she must forage to compensate for those losses (see Millar 1978; Mendl 1988). Lactation can significantly increase the mortality rates of females (Clutton-Brock et al. 1989) and higher suckling rates can inflict higher costs (Nicolson 1987).

Many authors have therefore considered non-offspring nursing to provide an example of altruistic behaviour that has evolved either through kin selection or reciprocity (e.g. Bertram 1976; Riedman 1982; Packer & Pusey 1984; Wilkinson & Baker 1988; Hoogland et al. 1989). However, other authors have considered it to result from parasitism by the young (e.g. Reiter et al. 1978; McCracken 1984) or misdirected maternal care (e.g. Fogden 1971; Boness 1990).

Non-offspring nursing has been reported in virtually every major taxonomic grouping of mammals (see below), but the extent of the behaviour varies greatly from taxon to taxon. Comparative studies may therefore provide important insights into alternative hypotheses for the evolution of non-offspring nursing. While there are potential problems from relying on behavioural observations of nursing to estimate the quantity of milk transferred to each infant (see Mendl & Paul 1989), differences in the frequency of non-offspring

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nursing across species should at least reflect differences in the opportunity for milk transfer to non-offspring.

In this paper we present a comprehensive statistical analysis of the extent and correlates of non-offspring nursing in 100 mammalian species. We base our analysis both on a literature review and on a widely distributed questionnaire. The questionnaire was essential to confirm that non-offspring nursing is absent in many species. We show that non-offspring nursing is more commonly observed in captive studies than in the wild. The most important factor influencing the extent and context of non-offspring nursing in the wild is litter size.

METHODS AND RATIONALE

Where possible, we extracted data on the incidence of non-offspring nursing from the literature. However, few published reports provide quantitative information on the frequency with which this behaviour occurs. Furthermore, a review based solely on the literature may well be biased because published reports are more likely to indicate the presence of non-offspring nursing rather than its absence.

We therefore distributed 135 questionnaires to field biologists working on a wide variety of mammalian species and received 92 replies. Researchers were requested to provide an approximate assessment of the behaviour of each species rather than a formal quantitative analysis. We emphasize that data gathered from the questionnaires must be viewed as tentative for any particular species; they were collected only to allow broad interspecific comparisons. The analysis is restricted to species that live in groups since these are the only species where young have the opportunity to nurse from females other than their own mothers (except as an artefact of captivity, e.g. Gemmell 1988). Appendix I lists the sources of information on each species and the data are presented in Appendix II. We present the modal response for species that have been studied by several investigators.

Respondents were asked to classify the proportion of time that young nursed from lactating females other than their own mother. These classifications were as follows: (1) never; (2) $<10\%$ of total nursing time; (3) $>10\%$ of nursing time, but less than on its own mother; and (4) as much or more than on its own mother (see key to Appendix II). We requested that this information be reported on three different stages of development. However, most species could be observed for only one or two developmental stages and we have classified each species according to the maximum extent of the behaviour observed at any age.

To test specific hypotheses about the evolution of non-offspring nursing, we solicited information on the following factors.

(1) Nature of study: field or captive. Conditions of captivity may not reflect the ecological forces that have led to non-offspring nursing.

(2) Tolerance of females to nursing by non-offspring; whether females knowingly nurse non-offspring or whether the infant gains milk primarily by stealing it (for descriptions of such parasitism see Reiter et al. 1978; McCracken 1984).

(3) Whether females live in kin groups. Increased kinship should increase the females' tolerance for nursing by non-offspring (Hamilton 1964).

(4) Number of females in social group and number of lactating females in group. Many theoretical models emphasize that advantages of cooperation are greatest in small groups, as are coefficients of relatedness (see Discussion). Information on group size is thus an important indicator of the potential for cooperation in species where there are no data on kinship structure.

(5) Mother's diet. Costs of lactation may depend on diet; the need for communal care may be highest in species where food is difficult to obtain (Riedman 1982; Gittleman 1985).

(6) Temporal pattern of close proximity between mother and young; and between mothers. If communal care reduces the risk of starvation by minimizing the interval between meals (Caraco & Brown 1986), then non-offspring nursing should be more common in species where females spend long periods away from their young and return to their young asynchronously.

(7) Relative feeding success of different mothers. If non-offspring nursing minimizes variance in food intake, it should be most pronounced in species showing the highest variation in food intake by individual mothers.

(8) Litter size at birth and at weaning. Costs of care for additional young should decline with increasing litter size (see Discussion).

(9) Type of hiding-place/refuge for young. Misdirected maternal care may be highest in crowded areas or in species that keep their young in a dark den.

(10) Demographic correlates of females and young that engage in the behaviour (e.g. females that have lost young; young that have been orphaned; dominance and kinship relations between the donor and the recipient's mother; etc.).

STATISTICAL ANALYSIS

Interspecific comparisons are often hampered by the possibility that related species show similar adaptations through a shared phylogeny (Harvey & Mace 1982; Ridley 1983; Felsenstein 1985; Grafen 1989; Pagel & Harvey 1989; Harvey & Pagel 1991). This problem is especially acute in our study. Non-offspring nursing is ubiquitous in canids, for example, suggesting that the trait was present in a common ancestor. We therefore used phylogenetic regression (Grafen 1989) and evolutionary covariance regression (Pagel & Harvey 1989) models to locate independent evolutionary events.

These programs identify evolutionary changes in the dependent variable (at any taxonomic level) and specify whether these are associated with a concomitant change in the independent variable. A 'contrast' is positive if an increase in one variable is associated with an increase in the other variable. If the two traits are linearly related (e.g. a small increase in Y is associated with a small increase in X; and a large increase in Y is associated with a large increase in X), a regression of these contrasts will have a slope that is significantly different from zero and an intercept that passes through the origin (see Harvey & Pagel 1991).

There are several differences in the underlying assumptions of the two evolutionary regression models (Harvey & Pagel 1991; Grafen, in press). However, when employed in a simple regression analysis, both models always agree on the direction of a particular contrast although they often disagree on the magnitude of that contrast. In our analysis, whenever Harvey & Pagel's model showed a significant linear relationship that passed through the origin, the two models differed only slightly and we report the regression statistics from both models.

Because Grafen's method forces the regression through the origin, the two models identify certain significant relationships in different ways. If all contrasts have the same sign but the magnitude of the change in Y remains constant with increasing changes in X, Pagel & Harvey's model shows a regression slope that is not significantly different from zero. A significant relationship is detected by a binomial test of the signs of the contrasts. In our analyses of such cases, Grafen's model always gave the same result by sign-test, and the slope of the regression line was always significantly different from zero. Most of our results were of this type and we report them as sign-tests.

In two cases, Pagel & Harvey's model indicated a significant linear effect, but the regression line did not pass through the origin (e.g. a small increase in X was associated with an increase in Y, but a large increase in X was associated with a decrease in Y). Neither of these was significant by Grafen's model and there was no obvious biological explanation for either relationship. We therefore chose to ignore them; for a discussion of these sorts of statistical aberrations see Grafen (in press).

All reported probabilities are two-tailed.

RESULTS

Combining information from all sources, we collected data on 100 species in 14 orders. Of the factors listed in the Methods, only the following showed a statistically significant relationship with the degree of non-offspring nursing.

Non-offspring nursing is more common in studies of captive animals than in field studies (16 positive contrasts versus five negative contrasts, $P=0.026$, two-tailed sign test). This supports the contention of several authors that non-offspring nursing often appears to be an artefact of disturbance, crowding or captivity (e.g. Dittrich 1968; Fogden 1971). It also suggests that non-offspring nursing is more common in conditions where females have access to unlimited food. To exclude any effects of captivity, all of the following analyses are restricted to data collected from field studies of 82 non-domesticated species.

Non-offspring nursing is more common in taxa with larger litter sizes for four of six measures of litter size (Table I). Because litter size is a relatively conservative trait, this trend is apparent at a fairly high taxonomic level. For example, non-offspring nursing is more common in pigs than in other Artiodactyla, and more common in carnivores and rodents than in primates or bats. Although taxa with larger litter sizes generally show higher levels of non-offspring nursing than related taxa with small litter sizes, Pagel & Harvey's model indicates that the two variables are not linearly related. A

Table I. Effect of increased litter size on extent of non-offspring nursing

Litter size	Increase	Decrease	*P* (sign test)
At birth			
Median	13	1	0·002
Minimum	7	2	NS
Maximum	14	2	0·004
At weaning			
Median	12	0	0·003
Minimum	4	2	NS
Maximum	12	2	0·012

Each independent contrast in which the level of non-offspring nursing is higher in the taxon with the larger litter size is listed as an 'increase' (positive contrast); each contrast where the level of non-offspring nursing is lower in the taxon with the larger litter size is a 'decrease' (negative contrast). The contrasts thus show that taxa with larger litters engage in higher levels of non-offspring nursing.

Table II. Effect of increased degree of 'milk theft' on extent of non-offspring nursing

Taxa	Increase	Decrease	*P* (sign test)
Monotocous	11	1	0·006
Polytocous	2	5	NS
	$P<0{\cdot}02$, Fisher test		

Increase and decrease are as defined in Table I. The contrasts show that theft is associated with a high degree of non-offspring nursing in monotocous taxa, but not in polytocous taxa and that monotocous taxa show a greater increase than polytocous taxa.

large increase in litter size is not associated with a larger increase in non-offspring nursing than is a small increase in litter size. We therefore controlled for the non-linear effect of litter size by performing all further analyses separately for monotocous taxa (those that typically give birth to only one young; $N=52$ species) and polytocous taxa (those that routinely give birth to multiple young; $N=30$ species).

Monotocous taxa appear to differ from polytocous taxa in the context of non-offspring nursing. Respondents were asked to assess whether females 'knowingly' nursed non-offspring; or whether the infants mostly gained milk by stealing it. Our analysis reveals that non-offspring nursing is generally associated with 'milk theft' in monotocous taxa, but not in polytocous species (Table II). This suggests that parasitic non-offspring nursing may be prevalent only in monotocous taxa.

Non-offspring nursing is more common in polytocous taxa that form smaller groups, whereas in monotocous taxa, non-offspring nursing is relatively more common in larger groups. This is true both for the median number of females in the group and for the median number of lactating females in the group (Table III). We present these results separately, even though the two measures of group size are highly correlated with each other.

Among monotocous taxa that show non-offspring nursing, non-offspring nursing is more common in taxa where a relatively high proportion of the behaviour involves females that have lost their own nursing offspring (9 of 10 signed contrasts, $P=0{\cdot}022$).

No further significant effects were found. However, pertinent data were usually unavailable for many detailed questions concerning the behaviour and ecology of each species. After controlling for field/captivity and for litter size, statistical tests could be based only on relatively few independent data points (a maximum of nine contrasts in polytocous species; 16 for monotocous species). There may also be numerous inaccuracies introduced by the qualitative nature of the questionnaire. It is therefore possible that there are many more factors influencing the incidence of non-offspring nursing than we have been able to detect.

DISCUSSION

Analysis of non-offspring nursing is complicated by the fact that a single behaviour may have different causes and effects in different species. At one extreme, non-offspring nursing may be advantageous to a parasitic infant but very costly to the female, while at the other extreme it could be advantageous to both mothers and young. Despite the limitations of our data, the analysis provides some insight into the distribution of this range of possibilities. Non-offspring nursing is most common in taxa with larger litter sizes. Non-offspring nursing is typically associated with milk theft in monotocous taxa, but not in polytocous taxa. The lower levels of non-offspring nursing in monotocous taxa may therefore result from a generally lower tolerance towards non-offspring by the

Table III. Effects of increased group size on extent of non-offspring nursing

				Regression model			
				Pagel & Harvey		Grafen	
Taxa	Increase	Decrease	*P*	r^2	*P*	r^2	*P*
No. of females per group							
Monotocous	9	4	NS				
Polytocous	1	7	0·070	0·436	0·027	0·258	NS
			$P<0{\cdot}05$, Fisher test				
No. of lactating females per group							
Monotocous	9	3	NS				
Polytocous	0	8	0·008	0·431	0·039	0·621	0·025
			$P<0{\cdot}01$, Fisher test				

Increase and decrease are as defined in Table I. The contrasts show that non-offspring nursing is most common in polytocous taxa that live in smaller groups, whereas it is relatively more common in monotocous taxa that live in larger groups.

lactating females. Thus 'parasitism' may be most widespread in monotocous taxa that form very large groups; and truly communal nursing (if it ever occurs) may be largely restricted to polytocous taxa that live in small groups.

Why should non-offspring nursing be more common in species with larger litters; and why should monotocous females be less tolerant of non-offspring nursing? There are several possible explanations. First, as litter size increases, it may be increasingly difficult for a female to recognize her own offspring or to restrict nursing access only to them. However, the incidence of non-offspring nursing in polytocous species declines with increasing group size although 'confusion' might be expected to be greatest in the largest groups.

Second, polytocous females may be more tolerant because, across species, the costs of non-offspring nursing decrease with increasing litter size. Twinning is uniformly rare in monotocous taxa; and it is very rare for both twins to survive (e.g. Haukioja et al. 1989). In contrast, most polytocous species show a distribution of litter sizes (Mendl 1988; for exceptions see Birney & Baird 1985). This suggests that there are strong constraints on monotocous females to care for a single young, whereas variability in litter size in polytocous species reflects differing optima under different circumstances.

In monotocous species, non-offspring nursing is generally rare and often involves females that continue nursing after the loss of their young. Monotocous females must therefore pay high costs for non-offspring nursing: if they simultaneously nurse non-offspring as well as their own, they must sustain food intake rates considerably higher than the presumed optimum; if they nurse the offspring sequentially, they must remain in the physiological state necessary for lactation, and, in many species, refrain from subsequent reproduction (e.g. Altmann et al. 1978; Louden et al. 1983; Stewart 1988). In contrast, a polytocous female that conceives fewer offspring or loses part of her litter during a temporary food shortage may often be able to produce more milk when conditions improve. Because she is obliged to continue lactating anyway, her only costs would come from the need to produce 'excess' milk. The relatively small costs of this excess would be reduced even further if it was invested in the young of her close relatives (see below) or if there were advantages to her own offspring from the improved survival of peers, e.g. through cooperation (Bertram 1976), thermoregulation (Sayler & Salmon 1970) or the dilution effect (Hoogland et al. 1989; Wilkinson, in press).

This pattern parallels the greater frequency of conspecific nest parasitism in bird species where hatchlings feed themselves compared with species with parentally fed young. Rohwer & Freeman (1989) reviewed evidence that intraspecific parasitism is widespread in such species because of the relatively low costs of misdirected parental care: parasitic self-feeding hatchlings inflict very small costs on the young of the hosts and require little additional effort to rear. Species with self-feeding young show far fewer defences against conspecific nest parasitism than species with parentally fed young.

Non-offspring nursing is most common in polytocous taxa that form small groups and this is consistent with models of cooperation based on kin selection, reciprocity or mutualism. Where females are philopatric (as is the case in most mammals, Pusey 1987), average kinship between females is expected to be highest where groups are smallest (Bertram 1976; Seger 1977; Murray 1985; Wilkinson 1987). Thus communal nursing may result from kin selection. However, reciprocity is also most likely to evolve in small groups (Boyd & Richerson 1988) and mutualistic advantages from cooperation are also highest in small groups (e.g. Pulliam 1973; Packer & Ruttan 1988; Lima 1989). Given the more parasitic nature of non-offspring nursing in monotocous taxa, it is noteworthy that the behaviour is comparatively more common in taxa that form very large groups (e.g. bats, pinnipeds). These are conditions where females would often be unrelated and social relationships unstable, and hence subject to greater parasitism.

Many of the questions in our survey were intended to disentangle the different routes to cooperation, but the available data on kinship and the behaviour of nursing females are inadequate to do so. For example, there are virtually no differences in kinship structure between most species of the same family and thus there are too few contrasts to provide a rigorous test.

Most mammals do form female kin groups (Greenwood 1980; Pusey 1987) and kin selection is the most plausible explanation for truly communal nursing. The most straightforward evidence for inclusive fitness effects would be that females clearly prefer to nurse the offspring of their closest relatives (Altmann 1979; Emlen & Wrege 1988). Although this sometimes occurs, many respondents indicated (anecdotally) that non-offspring nursing is apparently indiscriminate. Kinship effects could nevertheless be operating in such cases: females would not have to be highly discriminating if they were closely related to most females in their group. Future studies should test whether mothers are least discriminating in species where females are most closely related to each other on average.

In the absence of detailed behavioural data, we could test for evidence of reciprocity only by examining the larger question of whether 'cooperative' nursing minimizes the interval between meals. Caraco & Brown (1986) suggested that cooperative provisioning of young might evolve through reciprocity when breeders provision their young asynchronously. Cooperative provisioning does not increase the mean food intake of each young, but asynchronous communal provisioning would decrease the interval between meals thus reducing the risk of starvation. Because of the temptation for each parent to provision only its own offspring, cooperation between unrelated breeders could only be maintained by reciprocity. However, we could not find any relationship between inter-meal interval and non-offspring nursing. The extent of non-offspring nursing was not related to the degree of nursing synchrony nor to the duration of separation between mother and young. More direct tests for reciprocity are clearly needed.

Evolutionary analyses require information from a large range of taxa, and species that differ from the remainder of their taxonomic lineage are often the most informative. Thus, for example, while we received information on a wide variety of primate species, some of the most useful insights came from species that routinely give birth to twins. Although future behavioural studies of the causes of non-offspring nursing are likely to be most profitable on polytocous species that live in very small groups, useful insights could also be gleaned from species with unusual litter sizes or grouping patterns among their taxonomic group.

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APPENDIX I

Common name	Species	Source
Black-lipped pika	*Ochotona curzoniae*	A. Smith (personal communication)
Mexican free-tailed bat	*Tadarida brasiliensis*	G. McCracken (1984, personal communication)
Short-tailed fruit bat	*Carollia perspicillata*	T. Fleming (1988, personal communication)
Honduran white bat	*Ectophylla alba*	A. Brooke (1990, personal communication)
Greater spear-nosed bat	*Phyllostomus hastatus*	J. Bradbury (personal communication)
Fruit bat	*Pteropus poliocephalus*	Nelson (1965)
Pallid bat	*Antrozous pallidus*	Brown (1976)
Big brown bat	*Eptesicus fuscus*	Davis et al. (1968)
Serotine bat	*Eptesicus serotinus*	Kleiman (1969)
Noctule bat	*Nyctalus noctula*	Kleiman (1969)
Evening bat	*Nycticeius humeralis*	G. Wilkinson (in press, personal communication)
Pipistrelle bat	*Pipistrellus pipistrellus*	Kleiman (1969)
Mantled howler	*Alouatta palliata*	K. Glander (personal communication); Clarke & Glander (1981)
Red howler monkey	*Alouatta seniculus*	C. Crockett (personal communication); Crockett & Rudran (1987a, b)
Wedge-capped capuchin	*Cebus olivaceus*	T. G. O'Brien (1988, personal communication)
Squirrel monkey	*Saimiri sciureus*	S. Wiener (personal communication)
Green monkey	*Cercopithecus aethiops*	L. Fairbanks (personal communication)
Blue monkey	*Cercopithecus mitis*	T. E. Rowell & M. Cords (personal communication)
Patas monkey	*Erythrocebus patas*	J. Chism & T. E. Rowell (personal communication)
Rhesus macaque	*Macaca mulatta*	C. Berman & M. Champoux (personal communication); Berman (1982)
Bonnet macaque	*Macaca radiata*	J. Silk (personal communication)
Talapoin monkey	*Miopithecus talapoin*	J. Chism & T. E. Rowell (personal communication); Chism (1980)
Yellow baboon	*Papio cynocephalus*	J. Altmann & S. Wasser (personal communication)
Hanuman langur	*Presbytis entellus*	S. B. Hrdy (1977, personal communication)
Gelada baboon	*Theropithecus gelada*	R. Dunbar (1984, personal communication)
Humans	*Homo sapiens*	A. M. Hurtado & K. R. Hill (personal communication); Hurtado et al. (1985)
Ringtail lemur	*Lemur catta*	N. Collinge, L. Gould, P. Klopfer, M. Pereira & M. Sauther (personal communication); Pereira & Izard (1989)
Ruffed lemur	*Varecia variegata*	H. S. Morland & M. Pereira (personal communication); Pereira et al. (1987)
Gorilla	*Gorilla gorilla*	K. J. Stewart & A. H. Harcourt (1987, personal communication); Harcourt et al. (1981)
Chimpanzee	*Pan troglodytes*	A. E. Pusey (personal observation)
Coyote	*Canis latrans*	M. Bekoff (personal communication); Andrews & Boggess (1978); Camenzind (1978)
Wolf	*Canis lupus*	J. Packard (1980, personal communication); Paquet et al. (1982); Packard et al. (1985)
African wild dog	*Lycaon pictus*	J. Malcolm (personal communication)
Bat-eared fox	*Otocyon megalotis*	B. Maas (personal communication)
Red fox	*Vulpes vulpes*	Macdonald (1979); Macdonald & Moehlman (1982); Zabel & Taggart (1989)
Domestic cat	*Felis catus*	Macdonald et al. (1987)
Lion	*Panthera leo*	A. E. Pusey & C. Packer (personal observation)

APPENDIX I (*Continued*)

Common name	Species	Source
Dwarf mongoose	*Helogale parvula*	N. & S. Creel & J. Rood (personal communication)
Banded mongoose	*Mungos mungo*	J. Rood (personal communication)
Meerkat	*Suricata suricatta*	S. P. Doolan & D. W. Macdonald (personal communication)
Spotted hyaena	*Crocuta crocuta*	M. East, L. Frank, H. Hofer, K. Holekamp, G. Mills & L. Smale (personal communication)
Brown hyaena	*Hyaena brunnea*	G. Mills (1982, 1983, personal communication); D. & M. Owens (1984, personal communication); M. Knight & A. van Jaarsveld (personal communication)
California sea otter	*Enhydra lutris nereis*	M. Riedman (personal communication)
Coati	*Nasua narica*	J. Kaufman (personal communication); Russell (1983)
Galapagos fur seal	*Arctocephalus galapagoensis*	Trillmich (1981, 1984)
Northern fur seal	*Callorhinus ursinus*	Bartholomew (1959); Peterson (1968)
Steller sea lion	*Eumatopias jubatus*	L. V. Higgins (personal communication)
Australian sea lion	*Neophoca cinerea*	L. V. Higgins (personal communication)
California sea lion	*Zalophus californianus*	K. A. Ono (personal communication); Ono et al. (1987)
Grey seal	*Halichoeris grypus*	Kovacs (1987)
Weddell seal	*Leptonychotes weddelli*	D. Siniff (personal communication); Kaufman et al. (1975)
Northern elephant seal	*Mirounga angustirostris*	B. Le Boeuf (personal communication); Le Boeuf et al. (1972); Riedman & Le Boeuf (1982)
Cavy	*Cavia aperea*	Rood (1972)
Domestic guinea pig	*Cavia porcellus*	Fullerton et al. (1974)
Cuis	*Galea musteloides*	J. Künkele (personal communication); Rood (1972); Künkele & Hoeck (1987)
Dwarf cavy	*Microcavia australis*	Rood (1972)
Deer mice	*Peromyscus maniculatus*	King (1963)
Capybara	*Hydrochoerus hydrochaerus*	Macdonald (1981); Macdonald & Herrera (1984)
House mouse	*Mus musculus*	J. Manning & W. Potts (personal communication)
Black-tail prairie dog	*Cynomys ludovicianus*	J. Hoogland (personal communication); Hoogland et al. (1989)
Col. ground squirrel	*Spermophilus columbianus*	J. Waterman (personal communication)
Pronghorn	*Antilocapra americana*	J. Byers (personal communication)
Coke's hartebeest	*Alcelaphus buselaphus*	R. D. Estes (personal communication)
Bison	*Bison bison*	J. Berger & J. Wolff (personal communication)
Cattle	*Bos taurus*	L. Lidfors (personal communication); Lidfors & Jensen (1988)
Wild goat	*Capra aegagrus*	Schaller (1977)
Feral goat	*Capra hircus*	R. Dunbar & P. Klopfer (personal communication)
Wildebeeste	*Connochaetes taurinus*	R. D. Estes (personal communication); Estes & Estes (1979)
Bontebok	*Damaliscus dorcas*	David (1975)
Topi	*Damaliscus lunatus*	R. D. Estes (personal communication)
Grant's gazelle	*Gazella granti*	R. D. Estes (personal communication)
Thomson's gazelle	*Gazella thomsoni*	R. D. Estes (personal communication)
Roan	*Hippotragus equinus*	R. D. Estes (personal communication)
Sable	*Hippotragus niger*	R. D. Estes (personal communication)
Waterbuck	*Kobus defassa*	Spinage (1969)

APPENDIX I *(Continued)*

Common name	Species	Source
Oryx	*Oryx gazella*	R. D. Estes (personal communication)
Bighorn sheep	*Ovis canadensis*	J. Berger (1979a, b, personal communication); M. Festa-Bianchet (1988, personal communication)
Urial	*Ovis orientalis*	Schaller (1977)
Cape buffalo	*Syncerus caffer*	F. Mizutani (personal communication)
Greater kudu	*Tragelaphus strepsiceros*	N. Owen-Smith (personal communication)
Dromedary camel	*Camelus dromedarius*	Gauthier-Pilters & Dagg (1981)
Vicuna	*Vicugna vicugna*	Koford (1957)
Chital	*Axis axis*	Schaller (1967)
Red deer	*Cervus elaphus*	F. Guinness & M. Marquez (personal communication)
Reindeer	*Rangifer tarandus*	Epsmark (1971)
Giraffe	*Giraffa camelopardalis*	D. Pratt & V. Anderson (personal communication)
Warthog	*Phacochoerus aethiopicus*	Bradley (1968); C. Packer (personal observation)
Pig	*Sus scrofa*	P. Jensen (1988, personal communication); Eisenberg & Lockhart (1972); Bryant & Rowlinson (1984); Braun & Jensen (1988)
Collared peccary	*Tayassu tajacu*	J. Byers & J. Packard (personal communication); Byers & Bekoff (1981); Byers (1983); Babbitt & Packard (1990)
Southern right whale	*Eubalaena australis*	P. O. Thomas (personal communication)
Bush hyrax	*Heterohyrax brucei*	H. Hoeck (1977, personal communication); C. Magin (1987, personal communication); Hoeck et al. (1982)
Rock hyrax	*Procavia johnstoni*	H. Hoeck (1977, personal communication); C. Magin (1987, personal communication); Hoeck et al. (1982)
Horse	*Equus caballus*	S. Crowell-Davis (1985, personal communication); R. Keiper (personal communication)
Grevy's zebra	*Equus grevyii*	D. Becker (personal communication)
Asiatic elephant	*Elaphus maxima*	McKay (1973)
African elephant	*Loxodonta africana*	P. C. Lee (1987, 1989, personal communication)
Florida manatee	*Trichechus manatus*	T. J. O'Shea (personal communication)
Agile wallaby	*Macropus agilis*	Merchant (1976)
Whiptail wallaby	*Macropus parryi*	Kaufmann (1974)
Red-necked wallaby	*Macropus rufogriseus*	K. Higginbottom (personal communication)

APPENDIX II

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ochotona curzoniae	1	F	2	5	3·5				Y	N		S	1	8	5
Tadarida brasiliensis	1	F	10 000	2E+07	5E+06	10 000	2E+07	5E+06	Y	Y	I		1	1	1
Carollia perspicillata	1	F	2	18	3	2	18	3	N	Y	I		1	1	1
Ectophylla alba	1	F							Y				1	1	1
Phyllostomus hastatus	1	F	10	90	30					N			1	1	1
Pteropus poliocephalus	0	F		5000			5000		N	N-Y	I		1	1	1
Antrozous pallidus	0	F, C	10	100	45	10	100	45	N	Y	I		1	2	2
Eptesicus fuscus	0	F	13	92	33	13	92	33	N	Y	I		1	2	2
Eptesicus serotinus	0	C							N	Y			1	1	1
Nyctalus noctula	0	C		400			400		N	Y			1	3	1
Nycticeius humeralis	2	F	23	129		23	129		Y	N			1	3	2
Pipistrellus pipistrellus	1	C					200		N	Y			1	1	1
Alouatta palliata	1	F	2	16	7	2	10	4	Y	N		S	1	1	1
Alouatta seniculus	0	F	1	4	2	2	4	2	Y	N		S	1	1	1
Cebus olivaceus	2	F	2	10	5	2	5	3	N	N-Y	I	S	1	1	1
Saimiri sciureus	0	C	5	8	6	3	5	4		Y	S		1	2	1
Cercopithecus aethiops	1	C	3	12	6	3	12	6	Y	N		S	1	1	1
Cercopithecus mitis	0	F	9	18	13·5	2	6	4		N-Y			1	1	1
Erythrocebus patas	1	F, C	6	20	12	6	20	12	Y	N		S	1	2	1
Macaca mulatta	1	C	12	68	30	8	60	25	Y	N		UC	1	1	1
Macaca radiata	1	C	6	25		2	16		Y	N		S	1	1	1
Miopithecus talapoin	1	F, C						25	Y	N			1	2	1
Papio cynocephalus	0·5	F	2	22	20	2	12	5	Y	N		S	1	2	1
Presbytis entellus	1	F			8				Y	N			1	1	1
Theropithecus gelada	0	F	2	10	4	2	5	2	Y	N			1	1	1
Homo sapiens	0	F								N		UC	1	1	1
Lemur catta	1	F, C	2	8	3·75	2	7	3·25	Y	N			1	2	1
Varecia variegata	1·5	F, C	3	6	4·5	1	5	3	N	Y	I	S	2	4	2
Gorilla gorilla	0	F	2	10	4	2	10	4	Y	N		S	1	1	1
Pan troglodytes	0	F	4	20	12	2	8	6	N	N		S	1	2	1
Canis latrans	3	F	2	4	2	2	3	2	N	N			2	10	6
Canis lupus	3	F, C	2	2	2	2	2	2	N	Y	I		3	7	5
Lycaon pictus	3	F	2	6	3	2	2	2	N	N-Y	I	UC	3	14	10
Otocyon megalotis	3	F	1	2	2	2	2	2	Y	Y	I	S	2	5	2
Vulpes vulpes	3	F	2	4	2	2	2	2	N	Y	I	US	1	7	5
Felis catus	3	F	3	6	5	3	6	5	N	Y	I		1	5	4
Panthera leo	2	F	2	18	6	2	10	3	Y	Y-N	S	S	1	6	3
Helogale parvula	2·5	F	2	10	3·75	2	3	2	Y	Y	S		1	6	4
Mungos mungo	2	F	2	12	3·5	2	4	3	Y	Y					4
Suricata suricatta	2	F											2	5	4
Crocuta crocuta	0·5	F	2	30	19	2	17	8·5	N	Y	I	UC	1	3	2
Hyaena brunnea	1	F	2	5	2·5	2	2	2	N	Y	I	US	1	4	3
Enhydra lutris	1	F	2	40	6	2	20	3	N	N		S	1	1	1
Nasua narica	2	F	2	6	3·5	2	5	3·5	N	N			3	5	4
Arctocephalus galapagoensis	1	F							N	N-Y			1	1	1
Callorhinus ursinus	0	F	24	300		24	300		N	N-Y	I		1	1	1
Eumatopias jubatus	1	F	4	28	12	2	18	10	N	Y	I	UC	1	1	1
Neophoca cinerea	1	F	2	8	4	2	8	4	N	Y	I	UC	1	1	1
Zalophus californianus	1	F	50	300	200	20	250	100	N	Y	I		1	1	1
Halichoeris grypus	1	F	3	43	23	3	43	23	N	Y	I		1	1	1
Leptonychotes weddelli	1	F	42	88	65	42	88	65	Y	Y-N	I		1	1	1
Mirounga angustirostris	2	F	2	1000	200	2	800	180	Y	N		S	1	1	1
Cavia aperea	1	F											1	5	2
Cavia porcellus	2	C											1	5	2
Galea musteloides	3	F, C	4	8	6	2	6	4		Y	I	UC	1	6	2
Microcavia australis	3	F, C	2	3		2	3			Y	I		1	5	3
Peromyscus maniculatus	3	F, C	2	2	2	2	2	2	Y	N			3	7	4
Hydrochoerus hydrochaerus	2	F	2	8	5·5	2	8	5·5	Y	N					4
Mus musculus	3	C	2	5	4	2	4	2	Y	N		S	2	11	6
Cynomys ludovicianus	1	F	2	8		2	6		Y	Y	I	US			3
Spermophilus columbianus	0	F						35		Y	I	S			3
Antilocapra americana	1	F	5	20	12	5	20	12		Y	S	S	1	2	2
Alcelaphus buselaphus	1	F			4				N	Y	I		1	1	1
Bison bison	0·5	F	3	175	50	3	125	50	YN	YN			1	1	1
Bos taurus	1	C	65	445		65	445		N	Y	S	S	1	1	1
Capra aegagrus	0	F	2	50	5	2	30	5		Y-N			1	2	2
Capra hircus	0·5	F, C	4	50	7	2	7	2	N	YN	I	S	1	5	2
Connochaetes taurinus	1	F		1E+05	10				N	N-Y	I		1	1	1
Damaliscus dorcas	0	F	2	5	4	2	5	4	Y	Y-N	I		1	1	1
Damaliscus lunatus	0	F			5				N	Y	I		1	1	1
Gazella granti	0	F			10				N	Y	I		1	1	1
Gazella thomsoni	0	F			16				N	Y	I		1	1	1
Hippotragus equinus	0	F			5				N	Y	I		1	1	1
Hippotragus niger	0	F			15				N	Y	I		1	1	1

APPENDIX II *(Continued)*

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1	8	5	CD	CD	CD	GL	Y	Y									CR
			CD	CD	CD	I	N	Y							3	ND	NR
1	1	1	MG			FS	N										
1	1	1	CD, MG	CD, MG	CD, MG	FS		Y							3		
1	1	1	CD	CD	CD	FS	N										
1	1	1	MG	CD	CD	FS											
1	2		CD	CD	CD	I											
1	2		CD	CD	CD	I											
1	1	1	CD	CD	CD	I											
1	1	1	CD	CD	CD	I											
1	3	2	CD	CD	CD	I	N				0		1	1	2	ND	NR
1	1	1	CD	CD	CD	I									2		
1	1	1	MG	MG	MG	GL, FS	N		0	0	0	0	3	0	0		NR
1	1	1	MG	MG	MG	GL, FS	N						3				
1	1	1	MG	MG	MG	FS, I	Y	N	2						2	D=S	NR
1	1	1	MG	MG	MG	O											
0	1	1	MG	MG	MG	GL, FS, O	Y	Y	1		0	1	1	0	2	D=S	NR
1	1	1	MG	MG	MG	GL, FS, I											
1	2	1	MG	MG	MG	FS, I, O	Y	N	1		0	0	1	0	2	D=S	NR
1	1	1	MG	MG	MG	GL, FS, O	Y	N	2		2	0	2	0	2	D=S	CR
		1	MG	MG	MG	FS	Y	N	2		0	2		0	2	D=S	NR
1	2	1	MG	MG	MG	FS, I	Y	N	1		0	0	0	0	2	D=S	NR
1	1	1	MG	MG	MG	GL, FS, I	Y	Y	0	0	0	0	0	2	2	SND	NR
		1	MG	MG	MG	FS	Y	Y	0	0	0	0	0	3	0		
1	1	1	MG	MG	MG	GL	Y										
1	1	1	MG	MG	MG	O	YN										
1	2	1	MG	MG	MG	GL, FS	Y	N	1	0·5	0·5	0·5	0·5	0·5	2	D=S	NR
1	2	2	SD	SD	MG	FS		N	2	0	0	0	0	0	2	D=S	DR
1	1	1	MG	MG	MG	GL	N										
1	1	1	MG	MG	MG	FS, M, I	N										
		5	SD, CD	CD, MG	CD, MG	FS, M	Y	N							2	D=S	
3	4	4	SD, CD	CD, MG	CD, MG	M	Y	N	0	2	0	1	0	0	2	D=S	NR
6	16	10	SD	CD	CD	M	Y	N	2	2				2		D=S	CR
		2	CD	CD	CD	I	Y	N	0	0	0	0	0	0	3	D=S	CR
1	7	5	SD	CD	CD	M	Y		2						2	SND	CR
1			CD	CD	CD	M	Y	N		2		2			2		NR
1	4	2	SD	MG	MG	M	Y	N	1	2	0	1	1	1	2	ND	NR
1	6	3	CD	CD, MG	CD, MG	I	Y	N	2		1·5	0	1	0		SND	CR
1	16	3	CD	CD	CD	I	Y	N									
						I					1				2		
1	2	1	SD	CD	MA, MG	M	Y	YN	1	1	0	1	0	0	2		CR
1	3	2	SD	CD	CD	M	Y	N	1	0	0	0	0·5	0·5	2	SND	CR, DR
1	1	1	MA	MG	MG	I		Y	1				1				
0	4	2	SD, CD	SD, CD	MG	FS, I	YN	N	2						2	ND	NR
1	1	1	CD, MG	CD, MG	CD, MG	M, I		Y					2				
1	1	1	CD, MG	CD, MG	CD, MG	M											
1	1	1	CD	CD, MG		M	N	Y	0		0	0	2	0	1		
1	1	1	SD, MA	MA, MG	MG	M	N	N	1			0	1	1	2		
1	1	1	CD, MG	CD, MG	CD, MG	M, I		Y	1		0		0	0	1		
1	1	1	CD	CD	CD	M		N				2			2		
1	1	1	MG	CD, MG	CD, MG	M, I		Y				2					
1	1	1	MG	MG	MG	MF	N	Y	2			1	2	1	1	D=S	NR
						GL		N							3		
															2		
			CD	CD	CD	GL		YN	2	2		0	2	0	2	ND	
			CD	MG	MG	GL		N							2		
			CD	CD	CD	FS		N							3		
			SD	CD, MG	MG	GL		N							2	D=S	
0	8	3	CD	CD	CD	O		N	1	1	0	1	0	1	2	D=S	NR
1	6	3	SD	SD	CD	GL	Y		1	1	0	0	1	1	2		DR
1	5	3	SD	SD	SD	GL											
0	2	1	SD	MG	MG	GL	N	Y	1	0	0	0		2	2	D=S	NR
1	1	1	SD	CD, MG	CD, MG	GL	Y	N	3								
1	1	1	MG	MG	MG	GL	N	N	0	0	0	0	0	0	0	D=S	NR
1	1	1	CD	MG	MG	GL	Y	Y				1	1	0	2	D=S	
			SD	MG	MG	GL											
1	1	1	SD, MG	SD	MA, MG	GL	YN	N	1	1	0	1	1	1	1	D=S	
1	1	1	MG	CD, MG	CD, MG	GL	N	N					3				
1	1	1	SD	SD	MG	GL											
1	1	1	SD	CD, MG	CD, MG	GL	Y										
1	1	1	SD	CD, MG	CD, MG	GL	Y										
1	1	1	SD	CD, MG	CD, MG	GL	N										
1	1	1	SD	CD, MG	CD, MG	GL	Y										
1	1	1	SD	CD, MG	CD, MG	GL	Y										

APPENDIX II (*Continued*)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Kobus defassa	0	F							Y	Y-N	I		1	1	1
Oryx gazella	0	F			5				N	Y	I		1	1	1
Ovis canadensis	0	F	2	60	25	2	40	20	Y	YN	I		1	1	1
Ovis orientalis	0	F	2		3	2		3		Y-N			1	2	2
Syncerus caffer	1	C	5	62	28·5	4	13	4·5	Y	N		UC	1	1	1
Tragelaphus strepsiceros	0	F	2	10	3·5	2	8	2	Y	Y-N	I	S	1	1	1
Camelus dromedarius	0	F, C	2	15	5·5	2	7	2		N			1	1	1
Vicugna vicugna	0	F	2	16	5·5	2	9	4		N			1	1	1
Axis axis	1	C	2	70	3	2	45	3	N	Y-N	I		1	2	1
Cervus elaphus	0·5	F	2	25	12·75	2	25	12·5	Y	N		UC	1	1	1
Rangifer tarandus	1	C	6	6	6	6	6	6	Y	N			1	2	1
Giraffa camelopardalis	1	F	22	5	3	2	4	3	N	N		S	1	1	1
Phacochoerus aethiopicus	2	F	2	3	2	2	3	2	Y	Y-N		S	1	4	2
Sus scrofa	2	F, C	4	8	5·5	4	8	4·75	N	N		S	4	11	10
Tayassu tajacu	2	F, C	2	8	5	2	5	3	Y	N		S	1	3	2
Eubalaena australis	0	F							N	N			1	1	1
Heterohyrax brucei	1	F	2	6	3	2	6	3	Y	N		S	1	3	1
Procavia johnstoni	1	F	2	12	7	2	12	7	Y	N		S	1	4	2
Equus caballus	0·5	F	2	12·5	4·35	2	10	2	YN	N	I	US, S	1	1	1
Equus grevyii	0	F	2	8	4	2	8	4	N	N		S	1	1	1
Elaphus maxima	1	F				4	5	4·5	N	N			1	1	1
Loxodonta africana	1	F	8		4	8		3	Y	N			1	2	1
Trichechus manatus	1	F							N	N		S	1	2	1
Macropus agilis	1	C								N			1	1	1
Macropus parryi	0	F			18	10	16		N	N		S	1	1	1
Macropus rufogriseus	0	F			3			2	N	Y-N	I	US	1	1	1

APPENDIX II (*Continued*)

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1	1	1	SD	MG	MG	GL											
1	1	1	SD	CD, MG	CD, MG	GL	Y										
1	1	1	MA, MG	MG	MG	GL	YN										
			SD	MG	MG	GL											
0	1	1	MG	MG	MG	GL	N										
1	1	1	SD	MG	MG	GL	Y										
1	1	1	MA	MG	MG	GL											
1	1	1	MA	MG	MG	GL											
1		1	SD	MG	MG	GL		N	2						2		
1	1	1	SD	MG	MG	GL	Y	Y	0	0	0	0	0	0	3	D=S	
1	1	1	SD	MA	MA			Y	0	0	0	0	0	0	3		
1	1	1	MA	MG	MG	GL		Y	0	0	0	0	0	0	3	D=S	
0	3	2	SD	MG	MG	GL, FS	Y	N		2	0	0			2		CR
4	13	7	SD	MG	MG		Y	Y	2	2	0	0	0	2	2	ND	NR
1	2	2	MA, MG	MG	MG	GL, FS	Y	N				0		2	2	ND	CR
1	1	1	MA	MG	MG	I											
1	3	1	SD, CD	CD	CD	GL, FS		Y	0	2	0	0	3	0	0		
1	3	2	SD, CD	CD	CD	GL, FS		Y	0	0	0	0	3	0	0		
1	1	1	MG	MG	MG	GL	YN	YN	0	0	0	0	0	0	2	DNS	NR
1	1	1	MG	MG	MG	GL											
1	1	1	MG	MG	MG	GL											
1	2	1	MG	MG	MG	GL	Y	N	1						1	D=S	CR
1		1	MG	MG	MG	GL		YN	2							ND	NR
1	1	1	MG	MG	MG	GL		N							3		
0	1	1	MG	MG	MG	GL	Y										
		1	MG	MA, MG	MA, MG	GL	Y	N									

Key to Appendix II. (1) Extent of non-offspring nursing: 0 = Never; 1 = < 10% of total nursing time by young; 2 = > 10% of total nursing, but less than on own mother; 3 = as much as on own mother. (2) F = field, C = captivity. (3) Minimum number of females per group. (4) Maximum number of females per group. (5) Median number of females per group. (6) Minimum number of lactating females per group. (7) Maximum number of lactating females per group. (8) Median number of lactating females per group. (9) Do all of the lactating females remain together more than 75% of the time? Y = yes, N = no. (10) Do mothers spend less than 75% of each day with their young? Y = yes, N = no; N-Y = not during early lactation, yes during late lactation; Y-N = yes during early lactation, not during late lactation. (11) If lactating females spend time apart from each other and away from their young, do they return to their young: S = simultaneously, I = independently? (12) Daily feeding success of lactating females: UC = unequal and some females consistently feed more than others; US = unequal each day but similar over longer periods; S = similar each day. (13) Minimum litter size at birth. (14) Maximum litter size at birth. (15) Median litter size at birth. (16) Minimum litter size at weaning. (17) Maximum litter size at weaning. (18) Median litter size at weaning. (19) Where nursing young are kept at birth: SD = separate den, cave, beach or hiding spot that is inaccessible to other young; CD = communal den, cave, beach or hiding spot along with other young; MA = remains with mother, who remains apart from other young; MG = remains with mother, who continues to associate with others. (20) Where nursing young are kept during mid-lactation: classifications as in 19. (21) Where nursing young are kept during late lactation: as in 19. (22) Principal component of the mothers' diet during lactation: GL = grass or leaves; FS = fruits or seeds; M = meat; I = invertebrates; MF = mother fasts; O = other. (23) Do adult females typically form kin-groups? Y = yes, N = no. (24) Are most cases of the young nursing from another female the result of the young stealing milk? Y = yes, N = no. (25) Percentage of cases of non-offspring nursing that involve females that have lost all of their own litter: 0 = 0%; 1 = < 10%; 2 = > 10%; 3 = 100%. (26) Percentage of cases of non-offspring nursing that involve females that have lost part of their own litter: 0 = 0%; 1 = < 10%; 2 = > 10%; 3 = 100%. (27) Percentage of cases of non-offspring nursing that involve females that had not been pregnant that season (lactation without gestation): 0 = 0%; 1 = < 10%; 2 = > 10%; 3 = 100%. (28) Percentage of cases of non-offspring nursing that involve females that abandoned their young to be reared by other nursing females: 0 = 0%; 1 = < 10%; 2 = > 10%; 3 = 100%. (29) Percentage of cases of non-offspring nursing that involve young whose mothers have died: 0 = 0%; 1 = < 10%; 2 = > 10%; 3 = 100%. (30) Percentage of cases of non-offspring nursing that involve the young of one female supplanting the nursing offspring of another female: 0 = 0%; 1 = < 10%; 2 = > 10%; 3 = 100%. (31) Percentage of cases of non-offspring nursing that involve mothers that have not lost offspring and young whose mother is still lactating: 0 = 0%; 1 = < 10%; 2 = > 10%; 3 = 100%. (32) Is non-offspring nursing mostly by: SND = subordinate females nursing the offspring of dominant females; DNS = dominant females nursing the offspring of subordinate females; D = S = dominants and subordinates are equally likely to nurse each other's young; ND = dominance relationships not present. (33) Is non-offspring nursing: CR = restricted to the young of close female relatives ($r \geqslant 0{\cdot}25$); DR = restricted to the young of any female relative ($r > 0$); NR = extended to include the young of non-relatives. 'YN' indicates where two respondents gave different answers to a yes/no question.