Female space use is the best predictor of monogamy in mammals

PETR E. KOMERS[*,1,2] AND PETER N. M. BROTHERTON[2]

[1]*Department of Zoology, Section of Animal Ecology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden*
[2]*Large Animal Research Group, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK*

SUMMARY

Monogamy is typically considered to have evolved either because biparental care is important for offspring survival, or because males are unable to monopolize more than one female due to females being too dispersed. Here, in the first phylogenetic analysis of the evolution of monogamy in mammals, we show that neither of these explanations is consistent with the distribution of monogamy across mammal species. Monogamy evolved significantly more often in the absence of paternal care than in its presence. Furthermore, monogamy does not normally occur in species where female ranges are large. Rather, the most common feature of mammalian monogamy is that it evolved where females were solitary and occupied small, exclusive ranges, enabling males to monopolize them.

1. INTRODUCTION

Mammalian monogamy is puzzling because it is unclear what limits males to mating with a single female (Clutton-Brock 1989). Monogamy exists in nearly 5% of mammal species (Kleiman 1977) and numerous hypotheses have been proposed to explain its evolution (Gubernick 1994). The hypotheses largely relate to two types of monogamy, obligate and facultative (Kleiman 1977). Obligate monogamy is generally considered to evolve in response to a need for male care (Wittenberger & Tilson 1980; Clutton-Brock 1989; Gubernick *et al*. 1993). By contrast, facultative monogamy is thought to evolve when males are unable to monopolize more than one female because females are solitary and highly dispersed (Emlen & Oring 1977; Wickler & Seibt 1983). Although useful in emphasizing the diversity that exists within monogamous mating systems, the validity of the obligate versus facultative dichotomy has recently been challenged. Comparative studies show that paternal care does not correlate well with the occurrence of 'obligate' monogamy in primates (Wright 1990; Tardif 1994). In addition, monogamy in an ungulate where paternal care is absent does not seem to be 'facultative' because males do not attempt to monopolize more than one female, even when they are available (Brotherton & Rhodes 1996; Komers 1996).

Here, we present the first quantitative analysis of the relationships between paternal care, female dispersion, and monogamy across mammals. We use comparative methods to assess the validity of current theory, which suggests that either paternal care or female over-dispersion are the most general prerequisites for the evolution of monogamy.

2. METHODS

We obtained our data from secondary literature, but when available we added information from primary literature to resolve phylogenetic relationships of character state evolution (table 1). We used information from field studies for preference, because captive environments could affect social behaviour such as consortship and parental care. We included captivity data if field data were not available. Since it is not possible to measure paternal care as a continuous variable that would be comparable across distant taxonomic groups, we denoted paternal care as either present or absent. Paternal care was considered to be present if males of that species are known to retrieve young, transport young, or provide food. We considered it present irrespective of the intraspecific variation in the frequency of paternal behaviour exhibited (Kleiman 1977). Kleiman & Malcolm (1981) also included playing and socializing with young as forms of paternal care, but we have excluded these because it seems unlikely that fitness benefits from these behaviours would outweigh the benefits of reproducing with additional females. We concentrated on direct male care because it appears that it should be more likely for monogamy to evolve when paternal care is required and not shareable (Kleiman 1977; Kleiman & Malcolm 1981).

We use 'monogamy' to mean a social bond implying mating exclusivity. We use this definition because genetic evidence for mating exclusivity is rare in mammals. Extra-pair copulations have been observed in up to six monogamous species, but no extra-pair paternities were found in the three species for which genetic evidence of monogamy exists (Brotherton *et al*. 1997). We use the term 'paternal care'

Proc. R. Soc. Lond. B (1997) **264**, 1261–1270
Printed in Great Britain

1261

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Table 1. *Characters of mammalian species*

(MS = mating system; SC = sociality; OL = overlap of home range; PC = paternal care; DT = diet (only identified for species for which HR was known); BM = body mass (kg); HR = home range (ha); Ref = references; p = polygynous; m = monogamous; d = dispersed; g = gregarious; y = yes; n = no; C = carnivorous, O = omnivorous, H = herbivorous. See text for definitions. 'spp.' following a genus name refers to a group of species for which the character states were the same. These entries were used to resolve equivocal tracings of the character evolution. Entries with two letters represent reports of alternative character states.

	MS	SC	OL	PC	DT	BM	HR	Ref
Insectivora								
Sorex vagrans	p	d	y	n	C	0.010	0.32	4
S. araneus	p	d	n	n	C	0.010	0.05	4
S. minutus	p	d	.	n	C	0.010	0.11	4
S. obscurus	p	d	.	n	C	0.010	0.40	4
S. unguiculatus	p	d	.	n	C	0.013	0.05	21
S. gracillinus	p	d	.	n	C	0.004	0.03	21
S. caecutiens	p	d	.	n	C	0.007	0.02	21
Erinaceus europaeus	p	d	y	n	C	0.900	12.00	20
Macroscelidea								
Rhyncocyon chrysopygus	m	d	n	n	C	0.540	1.70	20,22
Macroscelides proboscideus	p	d	y	n	O	0.040	100.00	20,25
Elephantulus rufescens	m	d	n	n	C	0.037	0.24	20,22
Primates								
Galago senegalensis	p	d	.	y	O	0.200	2.60	16,28
Otolemur crassicaudatus	p	d	.	.	O	1.000	7.00	28
Galagoides alleni	p	d	y	.	O	0.260	12.00	28
Galagoides demidovii	p	d	y	.	C	0.060	1.00	28
Arctocebus calabarensis	p	d	.	.	O	0.300	10.00	28
Perodicticus potto	p	d	n	.	O	1.000	7.50	28
Microcebus murinus	p	d	.	.	O	0.060	1.00	11,28
Mirza coquereli	p	d	y	.	O	0.380	2.80	11,28
Lemur mongoz	m	d	.	n	.	.	.	28,34
Lepilemur mustelinus	p	d	n	.	O	0.600	0.20	11,28
Hapelemur griseus	m	d	.	y	.	.	.	28,34
Indri indri	m	d	n	.	O	10.500	18.00	11,28,33
Propithecus verreauxi	p	d	.	y	.	.	.	16,34
Avahi langier	m	d	.	n	.	.	.	16,20,34
Tarsius bancanus	p	d	n	n	C	0.110	1.50	23,28
Tarsius spectrum	m	d	n	n	C	0.150	1.00	12,28
Saguinus spp.	m	d	.	y	.	.	.	16,28,34
Leonthopithecus rosalia	m	d	.	y	.	.	.	16,28,34
Callithrix jacchus	m	d	.	y	.	.	.	16,28,34
Cebuella pygmea	m	d	.	y	.	.	.	16,28,34
Alouatta polioto	m	d	.	y	.	.	.	16,28,34
Alouatta spp.	p	g	.	n	.	.	.	16,28,34
Atelinae	p	g	.	n	.	.	.	16,28,34
Cebus albifrons	p	g	.	y	.	.	.	16,28,34
Saimiri sciureus	p	g	.	n	.	.	.	16,28,34
Aotus trivirgatus	m	d	.	y	O	0.950	10.00	28,34
Callicebus moloch	m	d	n	y	O	0.700	4.20	28,33,34
C. troquatus	m	d	n	.	O	0.700	2.10	28,33,34
Chiropotes spp.	p	d	.	n	.	.	.	16,20,28
Pithecia pithecia	m	d	.	n	O	1.500	7.00	11,16,28
Cercopithecus neglectus	m	d	.	n	O	4.000	10.00	11,28,33
Cercopithecus spp.	p	g	.	n	.	.	.	16,20,28,34
Erithrocebus patas	p	g	.	n	.	.	.	16,20,28,34
Macaca arctoides	p	g	.	y	.	.	.	16,20,28,34
M. fuscata	p	g	.	y	.	.	.	16,20,28,34
M. mulata	p	g	.	y	.	.	.	16,20,28,34
M. fascicularis	p	g	.	y	.	.	.	16,20,28,34
M. nemestrina	p	g	.	n	.	.	.	16,20,28,34
M. radiata	p	g	.	y	.	.	.	16,20,28,34
M. silvanus	p	g	.	y	.	.	.	16,20,28,34

(*Continued*)

Table 1. (*Continued*)

	MS	SC	OL	PC	DT	BM	HR	Ref
Papio anubis	p	g	.	y	.	.	.	16,20,28,34
P. cynocephalus	p	g	.	n	.	.	.	16,20,28,34
P. hamadryas	p	g	.	y	.	.	.	16,20,28,34
Theropithecus gelada	p	g	.	y	.	.	.	16,20,28,34
Presbytis melalopus	pm	gd	.	y	.	.	.	16,20,28,34
P. johnii	p	g	.	y	.	.	.	16,20,28,34
P. entellus	p	g	.	y	.	.	.	16,20,28,34
Hylobates agilis	m	d	n	yn	O	5.700	4.30	28,33,34
H. syndactylus	m	d	n	yn	O	10.600	18.00	28,33,34
H. klossii	m	d	n	yn	O	5.900	10.00	28,33,34
H. lar	m	d	n	yn	O	5.300	40.00	28,33,34
Gorilla gorilla	p	g	.	y	.	.	.	16,20,28
Pan troglodytes	p	g	.	y	.	.	.	16,20,28
Pongo pygmaeus	p	d	y	n	H	35.000	65.00	28,33
Lagomorpha								
Ochotona curzoniae	m	d	n	n	H	0.20	0.10	20,27
Sylvilagus aquaticus	p	d	y	n	H	2.30	4.00	20
S. floridanus	p	d	y	n	H	1.20	0.80	20
Caprolagus hispidus	m	d	.	n	H	2.50	0.28	20
Lepus timidus	p	d	y	n	h	3.00	3.70	14,20
L. europaeus	p	d	y	n	H	4.50	20.00	20
Rodentia								
Tamias striatus	p	d	y	n	H	0.10	0.40	11,19,20
Sciurus niger	p	d	y	n	H	0.95	6.50	11,19,20
S. carolinensis	p	d	y	n	H	0.55	1.90	11,19,20
Tamiasciurus hudsonicus	p	d	n	n	H	0.13	1.00	11,19,20
Castor canadensis	m	d	n	y	H	24.00	100.00	20
Pedetes capensis	m	d	.	.	H	3.50	6.00	3,20
Microtus pensylvanicus	p	d	.	y	H	0.045	0.03	16,17,20
M. californicus	m	d	.	y	H	0.04	0.00	16,17,20
M. montanus	m	d	.	y	H	0.03	0.00	16,17,20
M. ochrogaster	m	d	y	y	H	0.05	0.02	16,17,20
M. xanthognatus	p	d	.	.	H	0.10	0.20	17,20
M. agrestis	p	d	y	.	H	0.05	0.03	17,20
M. richardsoni	p	d	.	.	H	0.05	0.01	17,20
Ondatra zibethicus	m	d	n	y	H	1.10	1.20	11,18,20
Arvicola terrestris	p	d	.	.	H	0.16	0.50	20,29
Peromyscus leucopus	p	d	y	y	O	0.02	0.50	15,16,20
P. maniculatus	p	d	y	y	O	0.02	0.50	11,15,16,20
P. gossypinus	p	d	n	y	O	0.02	0.50	15,16,20
P. californicus	m	d	y	y	O	0.05	0.15	15,16,20
P. eremicus	m	d	n	.	O	0.02	0.30	15,20
Neotoma fuscipes	p	d	y	n	H	0.19	0.20	20,29
N. floridana	p	d	.	n	H	0.36	0.22	20
N. lepida	p	d	.	n	H	0.32	0.04	20
Onychomys leucogaster	m	d	n	y	C	0.05	2.50	20
Mus musculus	p	g	.	y	.	.	.	16,20
Rattus fucipes	p	g	.	n	.	.	.	16,20
Pseudomys albocinereus	p	g	.	y	.	.	.	16,20
Meriones unguiculatus	m	d	y	y	H	0.06	0.10	1,16,20
Tachyoryctes macrocephalus	p	d	y	n	H	0.60	0.11	20
Heterocephalus glaber	m	d	.	n	.			16,20
Atherurus africanus	m	d	.	y	H	2.70	6.70	5,20
Hystrix indica	m	d	n	y	H	14.00	80.00	20,26
H. africaeaustralis	m	d	.	y	H	20.00	260.00	5,20,31
Erethizon dorsatum	p	d	y	n	H	7.00	13.80	11,20
Coendou prehensilis	p	d	.	n	H	3.00	10.00	20
Microcavia australis	p	d	n	n	H	0.29	0.35	20
Dolichotis patagonum	m	d	n	n	H	12.50	11.00	20,30
Myocastor coypu	p	d	.	.	H	6.00	7.50	6,20

(*Continued*)

Table 1. (*Continued*)

	MS	SC	OL	PC	DT	BM	HR	Ref
Capromys melanurus	m	d	.	n	.	.	.	16,20
Octodon degus	p	g	.	n	.	.	.	16,20
Myoprocta exilis	m	d	y	n	H	1.20	0.90	8,16,20
Dasyprocta punctata	m	d	n	n	H	2.60	1.50	8,16,20
Agouti paca	m	d	.	n	H	9.00	4.50	16,20
Chinchilla lanigrea	p	g	.	n	.	.	.	16,20
Carnivora								
Vulpes vulpes	m	d	n	y	C	4.100	410.00	10,11,16,20
Vulpes cinereoargentes	m	d	.	y	O	3.700	110.00	10,11,16,20
Vulpes cana	m	d	.	y	C	1.000	160.00	11,16,20
Cerdocyon thous	m	d	n	y	O	6.000	150.00	10,11,16,20
Nictereutes procyuonides	m	d	.	y	O	5.000	2.80	10,11,16,20
Canis lupus	m	d	n	y	C	33.200	38100.00	10,11,16,20
Canis latrans	m	d	n	y	C	10.600	4200.00	10,11,16,20
C. aureus	m	d	n	y	C	8.800	1000.00	10,11,16,20
C. rufus	m	d	n	y	C	30.000	6100.00	10,11,16,20
Otocyon megalotis	m	d	n	y	O	3.900	70.00	10,11,16,20
Lyacon pictus	m	g	.	y	.	.	.	10,11,16,20
Ursus arctos	p	d	y	n	O	298.500	5310.00	10,11,16,20
U. americanus	p	d	y	n	O	110.500	5600.00	10,11,16,20
U. maritimus	p	d	.	n	.	.	.	16,20
U. ursinus	p	d	.	n	.	.	.	16,20
Bassariscus astutus	p	d	.	y	O	0.950	140.00	10,16,20
Procyon lotor	p	d	y	n	O	6.400	110.00	10,11,16,20
Nasua narica	p	d	.	n	.	.	.	16,20
Mustela erminea	p	d	n	n	C	0.960	14.00	10,11,16
Mustela vison	p	d	.	n	C	0.910	270.00	10,11,16
Martes martes	p	d	.	n	C	1.200	150.00	10,11,16
Martes americana	p	d	.	y	C	0.870	160.00	10,11,16
Martes pennanti	p	d	.	.	C	3.750	2590.00	10,11,16
Gulo gulo	p	d	y	n	C	11.620	38800.00	10,11,16
Ictonyx striatus	p	d	.	n	.	.	.	16,20
Meles meles	p	d	.	n	.	.	.	16,20
Arctonix collaris	p	d	.	n	.	.	.	16,20
Taxidea taxus	p	d	y	.	C	4.100	410.00	10,11,16
Mephitis mephitis	p	d	y	n	O	2.400	208.00	10,11,16
Lutra lutra	p	g	.	n	.	.	.	16,20
Pteronura brasilensis	m	d	.	y	.	.	.	16,20
Enhydra lutris	p	g	.	n	.	.	.	16,20
Lutrogale perspicillata	m	d	n	y	C	8.800	700.00	10,11,16
Nandinia binotata	p	d	n	n	O	3.200	73.00	10,11,16,20
Fossa fossa	m	d	.	n	C	1.800	100.00	10,11,16,20
Galidia elegans	m	d	.	y	C	0.810	23.00	10,11,16,17
Suricata suricata	p	g	.	n	.	.	.	16,20
Herpestes sanguineus	p	d	.	n	O	0.490	75.00	10,11,16,17
H. auropunctatus	p	d	.	.	O	0.780	31.00	10,11,16,17
Helogale parvula	m	d	n	y	O	0.270	30.00	10,11,16,17
Ichneumia albicauda	p	d	y	n	O	3.900	800.00	10,11,16,17
Cryptoprocta ferrox	p	d	.	n	.	.	.	16,20
Viverra zibethica	p	d	.	n	.	.	.	16,20
Civetictis civetta	p	d	.	n	.	.	.	16,20
Hyaena hyaena	p	d	y	y	C	26.800	5800.00	10,11,16,32
H. brunea	p	g	.	y	.	.	.	16,20
Crocuta crocuta	p	g	.	n	.	.	.	16,20
Proteles cristatus	m	d	n	n	C	8.300	100.00	10,11,16,20
Felis silvestris	p	d	y	n	C	4.700	100.00	10,11,16,20
Leptailurus serval	p	d	.	n	C	11.700	150.00	10,11,16,20
Puma concolor	p	d	y	n	C	51.800	4860.00	10,11,16,20
Lynx lynx	p	d	y	n	C	19.300	2240.00	10,11,16,20
L. rufus	p	d	n	n	C	6.200	3070.00	10,11,16,20
Panthera tigris	p	d	n	y	C	161.000	7140.00	10,11,16,20
P. pardus	p	d	n	n	C	52.400	2360.00	10,11,16,20

(*Continued*)

Table 1. (*Continued*)

	MS	SC	OL	PC	DT	BM	HR	Ref
P. leo	p	g	.	y	.	.	.	16,20
Acinonyx jubatus	p	d	y	n	C	58.800	6750.00	10,11,16,20
Artiodactyla								
Hyemoschus aquaticus	p	d	n	n	H	15.000	13.00	20
Okapia johnstoni	p	d	.	n	H	250.000	450.00	20
Cephalophus natalensis	p	d	.	n	H	13.000	8.50	2,20
C. dorsalis	p	d	.	n	H	21.000	40.00	9
C. callipygus	p	d	.	n	H	21.000	80.00	9
Philatomba monticola	m	d	n	n	H	5.000	2.90	2,7
Neotragus pygmaeus	p	d	y	n	H	2.500	11.00	20
N. batesi	p	d	y	n	H	2.500	3.00	20
Madoqua kirki	m	d	n	n	H	5.500	2.60	20
Oreotragus oreotragus	m	d	n	n	H	13.500	8.10	20
Redunca redunca	p	d	y	n	H	40.000	45.00	20
R. arundinum	p	d	y	n	H	78.000	74.00	20

References: (1) Ågren *et al*. 1989; (2) Bowland & Perrin 1995; (3) Butynski 1984; (4) Churchfield 1990; (5) De Villiers *et al*. 1994; (6) Doncaster & Micol 1989; (7) Dubost 1980; (8) Dubost 1988; (9) Feer 1989; (10) Gittleman & Harvey 1982; (11) Grant *et al*. 1992; (12) Gursky 1994; (13) Harestad & Bunnell 1979; (14) Johannessen & Samset 1994; (15) Kirkland & Layne 1989; (16) Kleiman & Malcolm 1981; (17) Madison 1985; (18) Marinelli & Messier 1993; (19) Merrit 1987; (20) Nowak 1991; (21) Ohdachi 1992; (22) Rathbun 1979; (23) Roberts & Kohn 1993; (24) Rood 1986; (25) Sauer 1973; (26) Sever & Mendelssohn 1991; (27) Smith & Wang 1991; (28) Smuts *et al*. 1986; (29) Southern 1979; (30) Taber & Macdonald 1992; (31) Van Aarde 1987; (32) Van Aarde *et al*. 1988; (33) Wrangham *et al*. 1993; (34) Wright 1990

to denote the care by the male which is socially bonded with the mother.

We used phylogenies of mammalian orders for which the existence of monogamy has been documented (table 2). We analysed alternative phylogenies presented for Carnivora (Wayne *et al*. 1989; Wozencraft 1989; Szalay *et al*. 1993; Garland & Janis 1993), for Rodentia (Avise *et al*. 1979; Rogers *et al*. 1984; Anderson 1985; Hartenberger 1985; Sarich 1985; Rogers & Engstrom 1992; Catzeflis *et al*. 1993; Nedbal *et al*. 1994), for Primates (Sillén-Tullberg & Møller 1993; Purvis 1995), for Artiodactyla (Garland & Janis 1993; Sæther & Gordon 1994; Gentry 1992), for Macroscelidea (Corbet 1995), and for Lagomorpha (Dene *et al*. 1982).

Table 2. *Phylogenetic analysis of the relationship between the evolution of monogamy and the occurrence of paternal care*

(The values represent the minimum and maximum number of origins derived in alternative phylogenies for the most parsimonious reconstructions, which either minimized or maximized (Maddison & Maddison 1992) the number of independent origins of monogamy or paternal care. Alternative combinations were derived by combining alternative phylogenies. Four alternative phylogenies were found for Primates and each of these was analysed separately for the situations where paternal care was assumed to be absent or present in *Hylobates*. This was done because of the considerable controversy on the importance of paternal care in *Hylobates* (Wright 1990; Dunbar 1988). Two differing alternatives were found for Rodentia*, while alternative phylogenies in the remaining orders did not produce differing reconstructions of the two character states, and all reconstructions were unambiguous.)

mammalian order	monogamy preceded by paternal care	simultaneous origins	monogamy in the absence of paternal care
Primates			
minimum	1–4	1–3	5–6
maximum	1–4	2–5	7
Rodentia			
minimum	1–2	1	2–4
maximum	2–4	1–2	3–4
Carnivora	0	4	2
Artiodactyla	0	0	3
Macroscelidea	0	0	2
Lagomorpha	0	0	2
total			
minimum	2–6	6–8	16–19
maximum	3–8	7–11	19–20

*The Neotominae–Arvicolinae clade of Rodentia includes a high proportion of species which show either monogamy or paternal care, or both, and within many reportedly 'monogamous' species there is a degree of variability, with some individuals mating polygynously or promiscuously (Cockburn 1988). It appears therefore that in *Microtus* and *Peromyscus* the assumption of independent evolution of either monogamy or paternal care is not justified, and that an ancestral species of these lineages may have had a tendency towards monogamy and paternal behaviour.

To investigate the evolutionary relationships between monogamy and paternal care, we used MacClade 3.0 (Maddison & Maddison 1992) and traced the evolution of paternal care and of monogamy (each as a binary character). Where the ancestry of a state was equivocal, we found the two most parsimonious reconstructions that either maximized or minimized the number of independent origins of monogamy and paternal care, respectively. We then used combinations of the alternative phylogenies for the maximized and minimized reconstructions, respectively. For each combination, we counted the number of times that monogamy was preceded by paternal care, evolved in the absence of paternal care, and the two characters evolved simultaneously (first appeared at the same branch node, table 2).

To compare the home ranges of females in monogamous species to those of closely related polygynous species, we included only species in which females are dispersed. Hereafter, we use 'polygynous' to imply any mating system in which males do not form an exclusive bond with a single female. We use 'dispersed' to mean the spatial distribution of independent females. Gregarious species were excluded from this analysis because our results from the above analysis suggested that monogamy does not seem to be viable in such species. Where the most closely related species exhibited the same mating system, their female home range sizes were averaged and compared to the most closely related group of species of the opposite mating system. We used these sister group comparisons (Purvis & Rambaut 1994) where the lines on a phylogenetic tree linking species or groups of species that are compared never meet or cross. In this method the comparisons are independent and take phylogenetic relationships into account (Harvey & Pagel 1991; Møller & Birkhead 1992).

Home range sizes (in ha) of species in which females are dispersed were taken from the literature (table 1). In species for which several studies reported home range size, mean values across studies were calculated. Where information on seasonal changes was provided, ranges during the reproductive season were used. Average female body mass (g) was taken from general reviews, if available (table 1). When information on seasonality of body mass was provided, the mass during the reproductive season was used.

We used two measures of female range-size body mass relationships. In the first, we divided home range size by the body mass of females. In the second, we used the difference between the observed and predicted home range size. To calculate the latter, we used the relationships between home range, body weight, and trophic level (herbivore, omnivore, carnivore), as derived by Harestad & Bunnell (1979). The first measure may be preferable if the estimated relationship between body weight and home range is inaccurate (indeed, the predicted relationship consistently overestimated the home range of carnivores larger than 10 kg). The second may be preferable if home range size and body mass do not scale linearly, which would affect the result when species of different sizes are compared.

Range overlap was analysed as either present or absent. Non-overlapping home ranges were defined as overlapping by less than 5%. For the sister group comparisons, two taxa of the opposite mating system were compared in the exclusivity of their ranges. If they were both either exclusive or overlapping, the comparison was made at the next lower branch node and a decision was made on which mating system was more often associated with range overlap.

3. RESULTS AND DISCUSSION

In a three-factor analysis (Procedure Catmod, SAS Institute (1990)) we found that there was no three-way interaction between mating system, grouping pattern, and paternal care (d.f. = 1, χ^2 = 2.49, p = 0.12). There were also no significant two-way interactions between paternal care and grouping (d.f. = 1, χ^2 = 1.13, p = 0.28), and between paternal care and mating system (d.f. = 1, χ^2 = 1.79, p = 0.18), and no single effect of paternal care (d.f. = 1, χ^2 = 0.68, p = 0.41). There was, however, a significant interaction between mating system and grouping pattern (d.f. = 1, χ^2 = 12.4, p < 0.001). This was because monogamy essentially does not exist whenever females aggregate (with other than their own offspring), and because there is no significant tendency for paternal care to occur more in some mating systems.

In the following, we compared the number of times that monogamy evolved after the evolution of paternal care to the number of times that monogamy evolved in its absence. We excluded cases where paternal care and monogamy evolved 'simultaneously', because they do not provide support for a conclusion of the precedence of either character. A possible argument that in such clades monogamy evolved 'immediately' after the occurrence of paternal care is not supported by the observation that whole clades exist, such as the primate clade of *Papio* and *Macaca* (figure 1), where paternal care prevails and is presumably the ancestral state without leading to monogamy. In such clades monogamy only evolved in species in which females are dispersed, for example, in the monogamous population of *Presbytis melalopus* (figure 1).

In total, we found 64 different combinations of the alternative phylogenies, in 61 of which monogamy evolved significantly more often (binomial two-tailed tests, p < 0.05) in the absence of paternal care than in its presence. The three non-significant solutions (binomial two-tailed tests, $0.14 > p > 0.05$) were all from minimizations of independent origins, in which *Hylobates* was assumed to exhibit paternal care (table 2). In these three solutions, monogamy in the absence of paternal care was still more common. Given current knowledge of the character states and phylogenetic relationships, we conclude that in mammals monogamy in the absence of paternal care evolved significantly more often than in the presence of it. This conclusion is sustained in any combination of current hypotheses on phylogeny.

Monogamy and paternal care may still be associated, however, if monogamy evolved more often than would be expected by chance in lineages where paternal care is present. This includes cases where both characters appeared simultaneously. Using fully resolved phylogenies, we applied the Maddisons' concentrated changes test (Maddison & Maddison 1992) in mammalian orders where both characters evolved. The occurrence of monogamy in lineages with paternal care was not significantly different from random in either Rodentia (p = 0.24 to p = 0.87), Primates (p = 0.15 to p = 0.90), or Carnivora (p = 0.075), whether the number of independent origins was maximized or minimized. This suggests that the associated evolution of the two characters occurred by chance.

While our results do not support the hypothesis that the need for paternal care promoted monogamy, we may reverse the argument and test if monogamy promoted paternal care. In all combinations of phylogenies we found
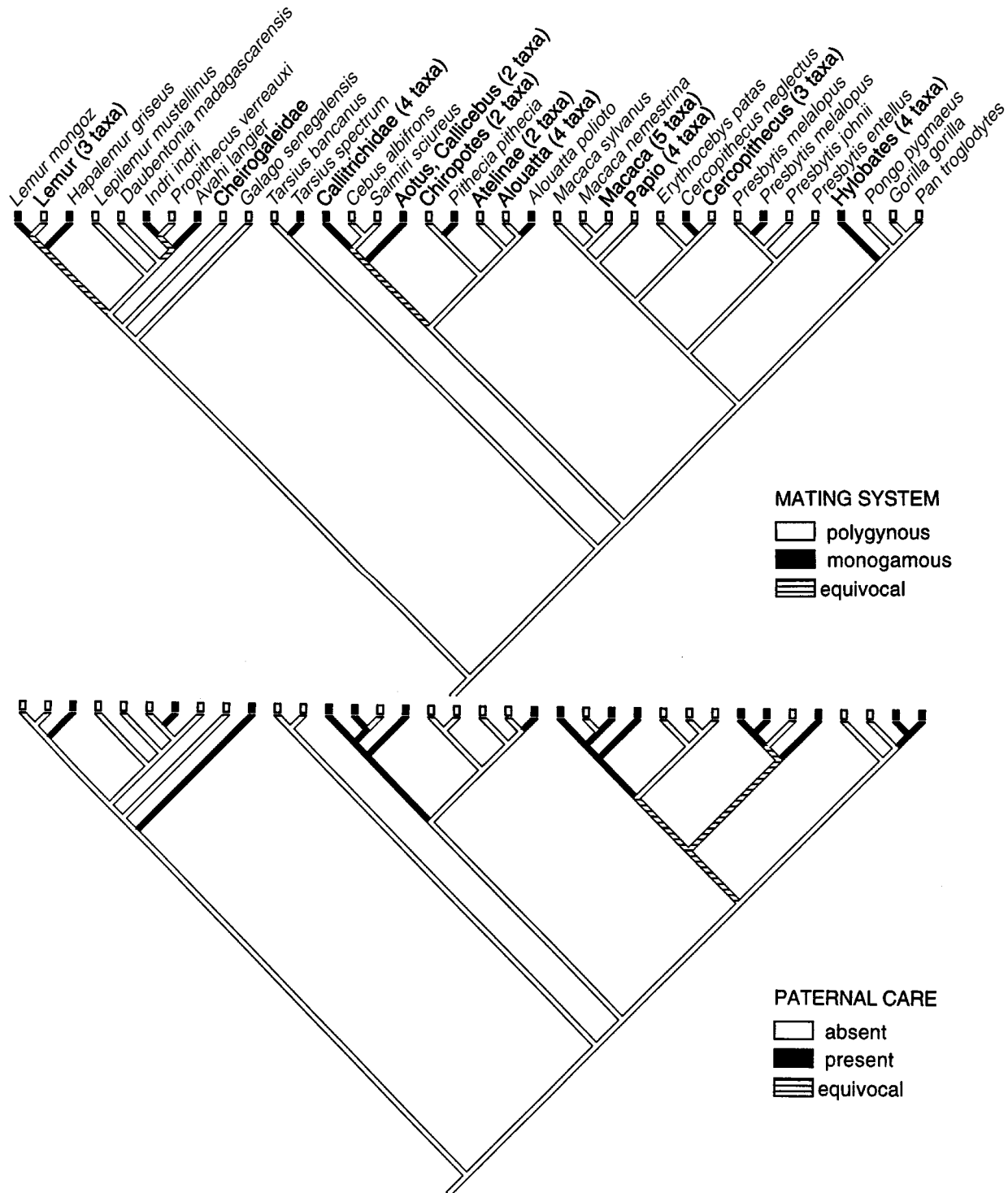
Figure 1. Reconstructions of the mating system and paternal care system in Primates on the phylogeny suggested by Purvis (1995). Sister taxa with the same character states were grouped for clarity. Polygynous mating systems include any system where males monopolize more than one female in one breeding season. There are two entries for *Presbytis melalopus* because it has been reported to have different mating systems in different populations.

that the evolution of monogamy was followed by that of paternal care a minimum of one and a maximum of three times. Comparing this to the number of times that monogamy was preceded by paternal care (minimum two, maximum eight, table 2), we found no combination in which either evolutionary sequence was predominant (binomial tests, two-tailed, $p > 0.12$). In fact, in six combinations both sequences were equally frequent.

These results support the finding that paternal care is a poor correlate of monogamy in primates (Wright 1990; Tardif 1994), and the statement can be extended to mammals as a whole. For a general theory on the evolution of monogamy in mammals, we must therefore focus on factors other than paternal care that may have promoted monogamy. We do not exclude the possibility that in some species males may be locked into

monogamy due to the need for paternal care. These species, however, must be interpreted as special cases rather than as representatives for a general rule (Dunbar 1988; Gubernick *et al*. 1993).

So far, we can reach the generality that monogamy in mammals is only viable where reproducing females are dispersed. This implies that monogamy occurs when males are unable to monopolize more than one female, perhaps because females are over-dispersed (Kleiman 1977; Emlen & Oring 1977). If the over-dispersion argument holds, monogamy should be more likely with increasing female dispersion. Although it has been shown for some primate species that monogamous ones do not have larger ranges than non-monogamous species (Dunbar 1988; Van Schaik & Dunbar 1990), the generality of this argument has not been tested.

Contrary to prediction, female home range was smaller in monogamous species in significantly more comparisons than vice versa, irrespective of the type of measurement of home range size (table 3). This conclusion remained unchanged when species with and without paternal care were analysed separately (table 3). If monogamy evolved where males are capable of defending one single female, monogamy should be more likely to evolve where female ranges do not overlap, because exclusive female ranges should be easier to monopolize than overlapping ones. In agreement with this, monogamous females occupied exclusive ranges more than females of polygynous species in 18 out of 19 sister group comparisons (binomial two-tailed test, $p < 0.001$). Considering only species with exclusive ranges, polygynous species used larger ranges than monogamous species (table 3). Monogamy was associated with exclusive ranges in both the presence and the absence of paternal care; monogamy was 2.6 times and 16.3 times more frequent (Fisher's exact, $p = 0.025$ and $p < 0.001$) in the presence and the absence of paternal care, respectively, when ranges were exclusive than when they overlapped.

In the above analysis we used home range size as a measure of dispersion. The two terms are clearly not synonymous because widely dispersed females can have either small or large ranges. However, our analysis of exclusive ranges (table 3) addresses this problem. Females with small exclusive ranges can be either widely dispersed or not. However, females with large and exclusive ranges can be only widely dispersed. On average then, the latter females should be more dispersed than the former, and if monogamy was associated with dispersion rather than range size, then these females should be more often monogamous. Our results point to the opposite.

Our results suggest that monogamy in mammals is promoted by females being solitary and occupying small and exclusive ranges. There is no evidence that monogamy evolved in response to the need for paternal care. Rather, it may be more likely that an association between fathers and offspring promoted the evolution of paternal care in species where both characters exist (Dunbar 1995). However, this may be true for both monogamous and polygynous systems where groups are stable and males are likely to associate with their own offspring. An alternative, and poorly tested hypothesis is that the care provided by the male is a form of his mating effort to attract females, which may prefer to mate with males that benefit the females' offspring (Smuts & Gubernick 1992). This hypothesis is based on the observation that male care does not correlate well with paternity certainty in primates (Wright 1990; Smuts & Gubernick 1992). This means that the term 'paternal' care should be more appropriately replaced by 'male' care in some cases.

The degree of sociality and ranging patterns of females affect the ability of males to monopolize them (Emlen & Oring 1977). While our results are contradictory to arguments which relate monogamy simply to over-dispersion of females (Emlen & Oring 1977; Cockburn 1988), they agree with the prediction that female ranges must be small enough for males to be able to defend them (Clutton-Brock 1989). However, given that monogamous species occupy smaller ranges than polygynous ones, it appears that monogamous systems should be prone to invasion by competitive roving males, particularly because females are less widely distributed. This is because the reward rate of finding receptive females should be higher where females are less dispersed. However, opting for

Table 3. *Results from sister group comparisons of home range size in monogamous versus dispersed polygynous species, using two estimates for home range (HR)*

(The values indicate the number of comparisons across six mammalian orders in which either polygynous or monogamous species used larger ranges. p values indicate the results from binomial two-tailed tests. W = body weight; a = proportionality factor, 0.002, 0.059, and 0.11 for herbivores, omnivores, carnivores, respectively; k = 1.02, 0.92, 1.36 for herbivores, omnivores, carnivores, respectively.)

	HR/W			HR-aWk		
type of comparison	polygynous	monogamous	p	polygynous	monogamous	p
all species ($n = 128$)	22	7	0.008	24	5	< 0.001
species with paternal care ($n = 35$)	6	0	0.032	5	1	0.22
species without paternal care ($n = 76$)	13	3	0.022	15	1	0.004
species with exclusive female ranges ($n = 45$)	10	1	0.012	9	2	0.066

monogamy under these conditions appears to be a strategy consistent with models which predict that animals are prone to exploit resources with the smallest possible variance, even at the expense of decreased mean reward (McNamara & Houston 1992). Provided that a single female can be monopolized successfully, monogamy can be viewed as a risk aversion strategy (McNamara & Houston 1992), because staying with one single female reduces the variance in mating success. Effective mate guarding would also increase the difficulty in finding receptive females. In addition, predation could represent a high cost of searching (Wrangham 1987; Goldizen 1987). The costs and benefits of monopolizing solitary females appear to be the primary issues in the evolution of monogamy in mammals. Benefits that females may receive from the male's proximity may represent additional spin-offs from this mating system. This argument could offer an explanation to the puzzling findings that monogamous males of some species appear to be capable of, but refrain from defending ranges large enough for two females (Dunbar 1988; Brotherton 1994; Komers 1996).

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