

An analysis and review of models of the sociobiology of the Mustelidae

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ABSTRACT

Classical models of social organization in mustelids suggest that female ranging patterns are determined by the dispersion of resources, whereas those of males are determined by the dispersion of females. However, mating systems and social spacing patterns vary widely both between and within species. For example, European Badgers exhibit a continuum from the classical mustelid model of intra-sexual territoriality and inter-sexual overlap to very large, mixed-sex, promiscuous groups. We evaluated hypotheses and existing data to explain this variation, using comparative analyses and Principal Components Analysis of life history and ecological variables. In addition, we applied a null model of allometric scaling to test for associations between group mass and residual home range size. We found that: (1) the degree of social behaviour and breeding group size increased with life history variables indicative of K-selected strategies of parental investment. (2) Absolute home range size and residual home range size (derived from allometric home range scaling) decreased, paradoxically, with breeding group size and group mass, respectively. These results provide support for ecological theories of social grouping in general and, in particular, for the importance of dispersed resource-rich patches as developed in the Resource Dispersion Hypothesis.

Keywords: Badgers, home range size allometry, life histories, mustelids, sociality, sociobiology

INTRODUCTION

Powell (1979) reviewed the sociobiology of the Mustelidae and concluded that, in general, the distribution and size of female home ranges were determined by resources, whereas male ranges were determined by the resulting female ranges. Sandell (1989) applied this model to all solitary carnivores, at least during the mating season (after Erlinge & Sandell, 1986). This is consistent with the established theoretical models of sexual differences in reproductive strategies in many other taxa (Trivers, 1972; Emlen & Oring, 1977; Davies, 1991). Female mustelids are principally concerned with defending a home range that provides enough food in which to rear offspring, whereas males maximize their reproductive success by encompassing as many mates in their range as possible. Consequently, male ranges are also ultimately determined, albeit indirectly, by food. This spacing pattern typically results in intra-sexual territoriality, which is also the most common sociobiological organization in the Ursidae, Procyonidae, Viverridae and Felidae (Kruuk & Macdonald, 1985). Clearly, social species violate this 'classical' model. Identifying which constraints are breached to permit sociality, a trait unusual among both the Mustelidae and the Carnivora as a whole (Gittleman, 1989), may provide a more thorough understanding of the classical model of intra-sexual territoriality.

Accumulating research has shown that the classical model can also be broken within species, supporting modern theory that mating systems result from individual strategies rather than being an evolved feature of each species (Clutton-Brock, 1989). Variation between populations highlights a remarkable flexibility in mustelid social organization and behaviour. For example, Badgers *Meles meles* in Britain normally form multi-male, multi-female groups (Woodroffe & Macdonald, 1993; Neal & Cheeseman, 1996). Paternity within groups is mixed, and immigrants often gain successful matings (Evans, Macdonald & Cheeseman, 1989; Cresswell *et al.*, 1992). In contrast, studies from elsewhere in their range show that they commonly live solitarily, or in pairs with either intra- or inter-sexual territories (Woodroffe & Macdonald, 1993; Rodríguez, Martín & Delibes, 1996; Revilla, 1998; Revilla *et al.*, 1999).

Erlinge & Sandell (1986) have also proposed complications to the intra-sexual territoriality model. They reviewed evidence showing that the movement patterns of male Stoats (*Mustela erminea*) changed radically in the mating season, and attributed this change to a switch in the critical resource, from food to mates. They argued that this resulted in two different 'social structures' for males, depending on the time of year (Erlinge & Sandell, 1986). All home range data may therefore be confounded according to the season in which the study was conducted. Stoats (Erlinge & Sandell, 1986; Sandell, 1986), Weasels *Mustela nivalis* (Erlinge, 1974; Moors, 1974) and American Mink *M. vison* (Gerell, 1970; Birks, 1981; Dunstone, 1993) all defend intra-sexual ranges, and those of males are much larger than those of females, so some contain two or more females even in the non-breeding season. However, in Stoats, male home ranges were either enlarged or abandoned altogether during the breeding season, perhaps because, for some lower-ranking individuals, receptive females became an economically indefensible resource (Erlinge & Sandell, 1986).

Territories encompassing more than two female ranges in the non-breeding season are presumably not for mating purposes, as implied by Erlinge & Sandell's (1986) 'flexible' territorial model. Alternative explanations are therefore needed. Testable hypotheses might be, for example, that male home ranges are simply larger than female ranges in the non-breeding season because of greater metabolic needs, and overlap those of females because of similar habitat preferences. Alternatively, males may be defending future potential mates during this period. Schröpfer, Wiegand & Hogrefe (1997) suggested that non-breeding season territoriality could be explained as male defence of offspring from infanticide. However, this would only be a useful strategy if they have some certainty of paternity (Ebensperger, 1998). Although we know of no evidence of this behaviour in mustelids, circumstantial support for this theory comes from the fact that in many animals (Birkhead & Møller, 1998), including American Mink (Venge, 1971), sperm from the last male to mate are more likely to fertilize the available ova. It is therefore conceivable that males stay near the females they mated with last at the end of their breeding season. However, this latter hypothesis is not supported by recent genetic data on mink (N. Yamaguchi & D. Macdonald, unpublished data).

Social spacing and mating systems are intertwined, as mating systems are effectively a result of the distribution of individuals, which may be imposed upon them by other factors such as resources (Alexander, 1974; Clutton-Brock & Harvey, 1978; Davies, 1991). Several authors have made very broad classifications of mating systems in mustelids: such that all mustelids are polygynous (Moors, 1980) or that all weasels are polygynous (Ralls & Harvey, 1985) and that all the Mustelinae defend intra-sexual territories (Powell, 1979). Estes (1989) categorized mustelids into three broad groups: (1) terrestrial mustelids – promiscuous or weakly polygynous; (2) freshwater otters – monogamous/promiscuous or weakly polygynous (in both of these first two classes, all females and some males were said to hold intra-sexual territories); and (3) sea otters – polygynous with territoriality among males only.

Development of these models, combined with the demonstration of widespread sperm competition (Møller & Birkhead, 1989) and the apparent flexibility of social behaviour (Macdonald, 1979, 1983; Hersteinsson & Macdonald, 1982; Hornocker, Messick & Melquist, 1983; Woodroffe & Macdonald, 1993; Creel & Macdonald, 1995), provides challenges for further study and re-evaluation of social spacing and mating systems. Tests of hypotheses explaining sociobiological patterns are suited to, or may in fact demand, new technologies. Video observation (Stewart, Ellwood & Macdonald, 1997b), GIS-based habitat analysis (Barreto, 1998) and paternity analysis (Evans *et al.*, 1989) using DNA microsatellite assays, are examples of new methods which may lead to a clearer understanding of social organization among mustelids.

Variation in social organization may be caused by environmental factors, intra- and inter-specific competition or phylogenetic inertia. In order to review these subjects, we discuss hypotheses for given aspects of sociobiology, and conduct our own inter-specific comparative analyses using a new data set and phylogeny. We present a general analysis of correlates of sociobiology, an analysis of the determinants of sociality using a null model based on allometric scaling and end with a brief case study of intraspecific variation in European Badgers.

I. INTER-SPECIFIC CORRELATES OF SOCIOBIOLOGY

Methods

We conducted a literature search to compile a database of life history variables for all of the mustelids (Appendix 1). For several species, few data are available. The wide intraspecific variation in carnivore social behaviour (e.g. Macdonald, 1979, 1983; Gittleman & Harvey, 1982; Creel & Macdonald, 1995) ensures an inevitable degree of error in using summary data. We tried to take the most recent data available for each species, although in some cases older data with larger sample sizes were deemed better. References for these appear as a superscript number in Appendix 1 and are detailed in Appendix 2.

The following continuous variables were analysed: (1) breeding group size; (2) female mass in kg; (3) group mass in kg (group size \times female mass; using female mass underestimates actual group mass, but maintains consistency with other female variables); (4) male mass in kg; (5) mean adult mass (female mass + male mass)/2 in kg; (6) sexual mass ratio (male mass/female mass); (7) home range in km². [Territories *per se* are difficult to define for many species (Johnson, 1973; King, 1975; Macdonald, 1980), so we used home range in preference]; (8) length of delay between fertilization and implantation, in days; (9) gestation in days, defined as the period between implantation and parturition; (10) litters per year; (11) litter size; (12) lactation period in days; (13) time to sexual maturity in months and (14) longevity in months. The following dichotomous or ordinal variables were also assessed: (15) ovulation type; (16) seasonal breeding; (17) social class; (18) carnivory; (19) diet class and (20) delayed implantation. Finally, we analysed some distributional data: (21) central latitude in degrees, at the centre of distribution and (22) maximum latitude at the furthest edge of distribution, measured in absolute degrees north or south of the equator. Latitudinal data were taken from Hall & Kelson (1959), Macdonald & Barrett (1993), Mason & Macdonald (1986) or *Mammalian Species* accounts. For disjunct distributions, we took the northern limit of northern area, and the southern limit of its southern area, the centre was the mean of these. Two species (*Gulo gulo* and *Mustela erminea*) live on different continents and have different latitudinal limits on each. We used the means of the limits of both distributions and the centre was the mean of those. The distributions of introduced populations, e.g. Weasels and American Mink, were not used. Other data from introduced populations (e.g. New Zealand) were also

avoided, as variables from those regions are not necessarily predicted to correlate with life-history variables evolved elsewhere under different conditions.

Where several estimates existed for a given variable, we used the mean. Where these were from more than one study, we used a mean of means. We used only female mass and home range to avoid the confounding influence of sexual selection on male mass or a mean of both sexes. Using mean mass for both sexes would be hard to interpret because of the variation in the degree of dimorphism among species, and mate searching strategies of males, which may vary independently of the factors under test here. We have referenced all data individually so that future studies can make use of our database. Some data columns are far from complete, but we have included them so that other authors can reference the data for which we did find confirmation.

Comparisons of life-history variables were made using three statistical methods. First, Principal Components Analysis (PCA) on the correlation matrix was applied to summarize the variance in life-history variables among species. Data were untransformed, no rotation was used and cases with missing values were omitted. We then tested for variation in the Principal Component scores using a one-way ANOVA with social class as a factor. Social class was a classification following Ortolani & Caro (1996) comprising: (1) solitary, (2) pairs, (3) variable groups, and (4) groups. We rejected sociality/non-sociality as a classification because of intraspecific variation. Some variables were not entered into the PCA because too few data were available. Eight variables for 33 species were used in the final analysis.

Second, simple or partial linear regressions of raw species data were conducted with breeding group size as the dependent variable. We controlled for body size differences between species by statistical removal of variation due to body mass alone, which was done by entering body mass first in a multiple regression.

Third, simple or partial linear regressions were conducted as before, but using Comparative Analyses by Independent Contrasts (CAIC) (Harvey & Pagel, 1991; Garland, Harvey & Ives, 1992). The CAIC method must be used in comparative studies, as raw species data are not statistically independent because related species may share traits due to common ancestry rather than to adaptation. Independent contrasts analysis controls for this by calculating the differences between log-transformed variables of pairs of sister taxa in the phylogeny. These can then be analysed using normal statistical methods to test whether a change in one variable is correlated with a change in the other (Harvey & Pagel, 1991), while holding constant the effects of body mass and forcing the regression through the origin (Harvey & Pagel, 1991; Garland *et al.*, 1992). Independent contrasts were calculated using the computer program 'CAIC version 2' (Purvis & Rambaut, 1994, 1995). CAIC performance is affected by the accuracy of branch length information, but not incompletely resolved trees (Purvis, Gittleman & Luh, 1994). We used a recent consensus phylogeny of the entire Carnivora (Bininda-Emonds, Gittleman & Purvis, 1999), for which the relationships between the Mustelidae are shown in Fig. 1.

Bonferroni corrections to significance levels are conservative because many of the variables used are likely to be intercorrelated. Therefore, we have presented unadjusted significance levels, but advise caution in their interpretation. Ovulation type and seasonal breeding were not analysed because fewer than three species exhibited one state of those traits. An extra term, gestation*lactation period, was included as a crude measure of maternal investment.

At the node above the Giant Otter *Pteronura brasiliensis* in the phylogeny provided by Bininda-Emonds *et al.* (1999), the calculated contrast for female mass is > 4 standard deviations from the mean. Therefore, this data point may be responsible for driving correlations. The large contrast is due to a combination of two unusual events: (1) the three daughter

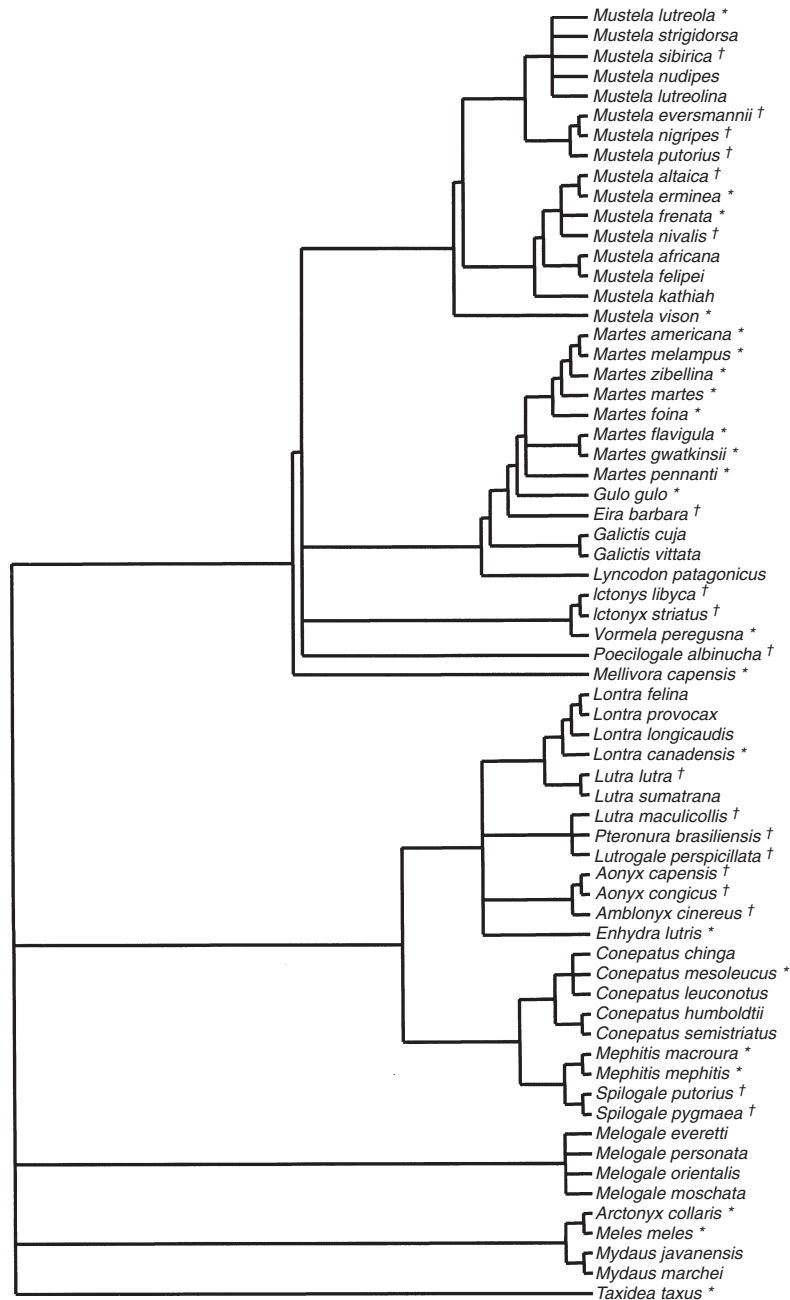


Fig. 1. Phylogeny of the Mustelidae after Bininda-Emonds *et al.* (1999). * = species with delayed implantation, † = species without delayed implantation, unmarked = unknown.

species diverged only recently and (2) the Giant Otter has evolved to be 4.4 times heavier during this time. This creates a large difference in masses between the three species branching from this recent node (Spot-necked Otter *Lutra maculicollis*, Indian Smooth-coated Otter *Lutrogale perspicillata* and Giant Otter). Therefore, we also calculated regressions using CAIC excluding data for this node.

Table 1. Summary of Principal Components Analysis. Variables with too few available data were not included

Variable	PC 1	PC 2
Eigenvalue	3.45	1.35
% of variance explained	43.1	16.9
Cumulative percentage of variance explained	43.1	60.0
Factor loadings		
Breeding group size	0.83	0.12
Female mass	0.92	0.11
Group mass	0.90	0.22
Sexual mass ratio	-0.56	0.55
Delay length	-0.05	-0.27
Gestation	0.66	-0.22
Litter size	-0.57	-0.28
Carnivorous*	-0.12	0.88

* Dichotomous variable

Results

The first two principal components together explained 60% of the total variance in the data for the 33 mustelid species that had complete data sets for the variables used (Table 1). The first principal component (PC 1) varied significantly between social classes (ANOVA, $F_{3,29} = 22.0$, $P < 0.0001$), but PC 2 did not (ANOVA, $F_{3,29} = 0.66$, $P = 0.58$) (Fig. 2). None of the other principal components varied significantly between social classes. The factor loadings of PC 1 indicated that the category of sociality was related to breeding group size, female mass, group mass, gestation period, sexual mass ratio and litter size. Carnivory and delay length were relatively unimportant in this axis.

Partial linear regressions for both raw data and independent contrasts using the continuous 'breeding group size' as the dependent variable are presented in Table 2. In previous analyses, the best correlates of mammalian life-history traits have been size, phylogeny and ecology (Gittleman, 1986, 1993). Using raw species data only, all variables involving mass were significant, except mean adult mass where female mass was statistically removed from the regression, and sexual mass ratio. Of all the other variables, only home range size and gestation*lactation were significant (negatively and positively, respectively). Using contrasts analysis, group mass was the only significant mass variable; other significant correlates of breeding group size using contrasts analyses were home range size, litters per year, lactation period (negative effect), gestation*lactation (positive effect) and longevity. When the contrast above the Giant Otter was removed from the analyses, group mass was the only significant variable.

II. ANALYSIS OF THE DETERMINANTS OF SOCIALITY

It is the social mustelids that deviate most from Powell's (1979) model, and these are considered in some detail in this section. Only 10–15% of carnivore species are social (Gittleman, 1989), and the causes of sociality have long been debated in the literature (Leyhausen, 1965; Alexander, 1974; Macdonald, 1983; Von Schantz, 1984a; Kruuk & Macdonald, 1985; Gittleman, 1989; Sandell, 1989; Blackwell & Bacon, 1993; Lindström, 1993; Woodroffe & Macdonald, 1993; Stewart, Anderson & Macdonald, 1997a). A recent review identified five principal situations favouring the evolution of sociality in carnivores (Creel & Macdonald, 1995):

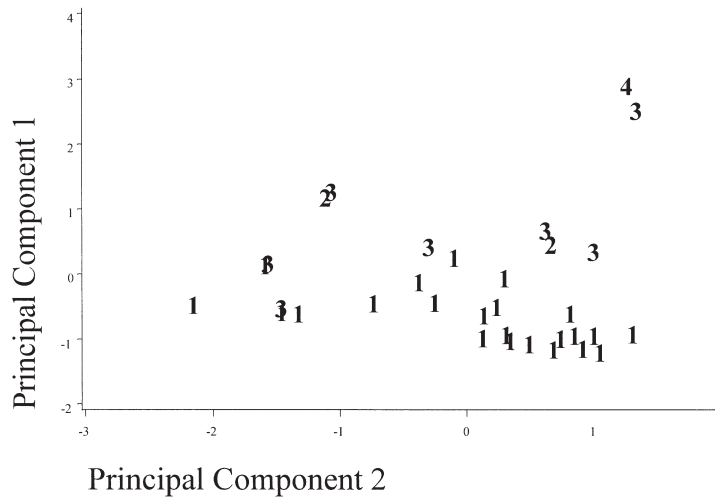


Fig. 2. Plot of the first two components from a Principal Components Analysis of life-history variables for 33 species of the Mustelidae. Numbers denote social class: 1 = Solitary, 2 = Pairs, 3 = Variable group, 4 = Group.

- 1 low cost of sharing range with conspecifics due to abundant, variable or rapidly renewing prey;
- 2 dispersal constrained by lack of suitable habitat, mates or high risk of mortality associated with competing conspecifics, predation or food scarcity;
- 3 benefits of intra-specific interactions, e.g. group hunting, group defence;
- 4 antipredator behaviour; and
- 5 alloparental care.

Although many studies have found significant relationships among life-history variables, ecological influences such as food supply and habitat suitability have rarely been good predictors of life history traits (see Gittleman, 1986, 1989, 1993; King, 1989a; Lessels, 1991) or social behaviour specifically (Chapman *et al.*, 1994; Creel & Macdonald, 1995). The apparent lack of an association between social behaviour and ecology may be partly because most life-history data can be easily quantified, whereas ecological data must often be gained via surrogate criteria (Creel & Macdonald, 1995). These criteria may be too crude to identify any complexities in space and time (Lindstedt, Miller & Buskirk, 1986; Woodroffe & Macdonald, 1993). An added problem, particularly for carnivores, is that contemporary distributions no longer accurately reflect the environment in which each species evolved, so correlations between life-history and ecological variables may not necessarily be expected. As a novel attempt to avoid these problems, we have applied a null model of social spacing, based on allometry, and have used the variation around the expected fit and information on individual species to test for an ecological explanation of sociality.

In classifying whether a species of mustelid is social or not, we followed Creel & Macdonald (1995): non-social species are uni- or bi-parental breeding groups; social species are those in which at least two adults of the same sex commonly share a range during breeding. In this family, the only known social species are the Sea Otter *Enhydra lutris*, the Oriental Short-clawed Otter *Amblonyx cinereus*, the Spot-necked Otter *Lutra maculicollis* (Ortolani & Caro, 1996), the Giant Otter *Pteronura brasiliensis* (Macdonald, 1992; Carter & Rosas, 1997; Ortolani & Caro, 1996) and certain populations of the European Badger (Woodroffe

Table 2. Life history and ecological correlates of breeding group size, using both species data and independent contrasts. All continuous variables were log-transformed (except central latitude, which has negative values). Partial linear regression controlling for female body mass in all cases, except for variables involving masses in species data, where results both with and without statistical removal of female body mass are given. Unadjusted significance levels are shown and attention to the number of correlations is advised in their evaluation

Variable	No. of species	Independent Contrasts Analysis								
		Species data			All data			Excludes node above Giant Otter		
		d.f.	t	P	d.f.	t	P	d.f.	t	P
Female mass	37	35	4.49	< 0.0001****	26	1.47	0.153	25	1.43	0.166
Group mass	37	34	11.32	< 0.0001****	25	3.33	< 0.01**	24	2.44	< 0.05*
(Female mass not removed)	37	35	6.80	< 0.0001****						
Male mass	35	32	2.82	< 0.01**	24	- 1.33	0.196	23	- 0.21	0.838
(Female mass not removed)	38	36	4.16	< 0.001***						
Mean adult mass	35	32	1.19	0.241	24	1.2	0.242	23	- 0.19	0.854
(Female mass not removed)	35	33	4.46	< 0.0001****						
Sexual mass ratio	34	31	1.12	0.271	23	- 1.5	0.14	22	- 0.48	0.635
(Female mass not removed)	34	32	- 1.57	0.126						
Home range	20	17	- 2.91	< 0.01**	13	- 3.26	< 0.01**	12	- 1.22	0.244
Length of delay	34	31	- 0.83	0.412	22	- 0.372	0.713	21	- 0.21	0.839
Gestation period	35	32	1.96	0.059	23	0.362	0.721	22	0.69	0.496
Litters per year	34	31	- 0.94	0.355	22	- 3.63	< 0.01**	21	0.35	0.73
Litter size	36	33	- 1.09	0.285	24	- 0.26	0.799	23	- 0.4	0.692
Lactation period	26	23	1.66	0.111	16	- 2.38	0.03*	15	- 0.11	0.911
Gestation*lactation periods	26	23	2.67	< 0.05*	16	3.65	< 0.01**	15	0.11	0.911
Time to sexual maturity	22	19	- 0.48	0.638	13	- 2.1	0.061	12	0.19	0.85
Longevity	30	27	- 1.39	0.175	20	- 3.46	< 0.01**	19	- 1.14	0.269
Central latitude	34	31	0.08	0.936	-	-	-	-	-	-
Max. latitude	34	31	0.02	0.981	-	-	-	-	-	-
Carnivory (0,1)	12, 25	35	0.07 ^a	0.943	7	0.10 ^b	0.921	-	-	-
Delayed implantation (0,1)	18, 20	36	0.76 ^a	0.451	9	0.51 ^b	0.622	-	-	-

**** $P < 0.0001$, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

^a T -test (two-tailed) ^b One sample T -test (two-tailed).

& Macdonald, 1993) and European Otter *Lutra lutra* (Kruuk & Moorhouse, 1991; Ortolani & Caro, 1996).

As well as this definition of social species, we have used in our analyses ‘breeding group size’ (Creel & Macdonald, 1995), a continuous and less subjective measure than the dichotomous one of sociality. We demonstrate in this section that, paradoxically, breeding group size increases significantly with decreasing home range size, even after removing the effects of body mass, phylogeny and latitude. Possible explanations for this are discussed.

Background to allometric home range scaling

McNab (1963) showed that across the Mammalia, home range size (HR) can be predicted by a linear function of body mass (M): $HR = aM^k$. His results suggested an approximation to the metabolic scaling power $k = 0.75$, and Gittleman & Harvey (1982) later predicted carnivore home range size using a measure of group metabolic needs based on $k = 0.75$. This exponent has theoretical (Kleiber, 1975) and extensive empirical backing among mammals (Nagy *et al.*, 1999). Such analyses are likely to include some error because of intraspecific variation due to, for example, prey densities (King, 1975). Nevertheless, this allometric scaling has been similarly demonstrated for carnivores using many different data sets (Harestad & Bunnell, 1979; Damuth, 1981; Lindstedt *et al.*, 1986; Swihart, Slade & Bergstrom, 1988; Gompper & Gittleman, 1991), including one for predatory birds (Schoener, 1968; Jenkins, 1981). It therefore appears that intraspecific variation is too small to influence the overall outcome. Exponents have repeatedly been found to be > 1.0 in carnivorous species. Thus, home range size appears to scale allometrically with body mass, but at a greater rate than expected by basal metabolic rate or daily metabolic needs (Reiss, 1988). This is important to social biology because allometric relationships among the Carnivora appear to explain much of the variation in home range size, enough that Harestad & Bunnell (1979) remarked ‘behavioural phenomena need not be invoked’ to explain home range size, as they have elsewhere (e.g. Larter & Gates, 1990, 1994). More recently, Kelt & Van Vuren (1999) have shown that, although carnivore HR may indeed scale with body size, a minimum HR occurs at $M \sim 0.1$ kg and then scales with different (opposing) slopes either side of this ‘optimum’ (an energetic optimum defined by Brown, Marquet & Taper, 1993). This is a potential source of bias in analyses involving several small species. However, the mustelids have only one species (Weasel) that is < 0.1 kg, so our regressions are not subject to this.

Allometric home range scaling among the mustelids

We calculated a power function to predict home range in mustelids: $HR = 1.74M^{0.88}$ (Fig. 3a, $r^2 = 0.52$, $F_{1,18} = 19.5$, $P < 0.001$). The fit for non-social mustelids only is better: $HR = 2.26M^{1.31}$ (Fig. 3b; $r^2 = 0.78$, $F_{1,15} = 52.3$, $P < 0.0001$). The parameters of these regression models can be compared with other studies of ‘hunters’ (mammals which fed on seeds, fruits or mobile prey): $HR = 0.15M^{1.26}$ ($N = 12$, $r^2 = 0.68$; Swihart *et al.*, 1988); carnivores $HR = 1.70M^{1.03}$ ($N = 38$, $r^2 = 0.66$; Lindstedt *et al.*, 1986) and $HR = 1.37M^{1.37}$ ($N = 20$; $r^2 = 0.81$; Harestad & Bunnell, 1979; corrected by Lindstedt *et al.*, 1986); for predatory birds, the exponent was 1.39 (intercept not given, $N = 46$; Schoener, 1968). Of these published studies, the median intercept is 1.37 and the median exponent is 1.32. The non-social mustelid model has a slope that agrees well with these. Clearly, the social mustelids do not fit the allometric model – in fact they were always outliers whether using female mass (like Lindstedt *et al.*, 1986), group mass (like Grant, Chapman & Richardson, 1992), or after controlling for group size and metabolic rate (like Gittleman & Harvey, 1982).

Controlling for latitude, we found breeding group size to be significantly negatively

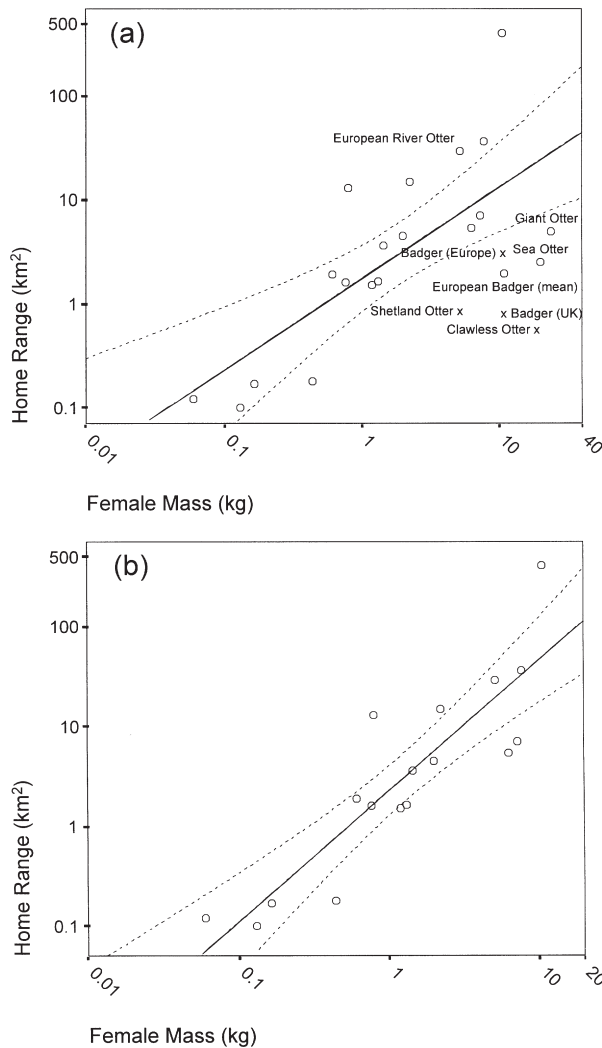


Fig. 3. Relationship between home range and body mass for (a) all species ($HR = 1.74 * M^{0.88}$, $P < 0.001$, X denotes species added *post hoc* for comparison only but not used in the regression) and (b) non-social species only ($HR = 2.26 * M^{1.31}$, $P < 0.0001$). Dotted lines are 95% prediction intervals of the mean predicted responses.

correlated with residual home range size (Fig. 4), using residuals from the allometric regression for all species described above. Thus, social species, such as the European Badger, Giant Otter and Sea Otter have a much smaller area of home range than would be expected from their mass. We repeated this analysis using the independent contrasts method and, controlling for body mass, again found a significant negative correlation between contrasts in group size and contrasts in residual home range size (Fig. 5). Absolute home ranges sizes were also significantly negatively correlated with breeding group size in the raw data and independent contrasts analyses (Table 2). These surprising results are conservative because (a) the social species reduce the slope below that expected for carnivores, and (b) because residuals are calculated using group home range size; if we use individual home range, which controls for predator biomass per unit area, the observed difference would be greatly enhanced.

One explanation for these relationships is that social mustelids are outliers only because, with increasing predator biomass, there is no necessary direct increase in required home range

Fig. 4. Regression of residual group size against residual home range size, $t = -5.02$, $d.f. = 18$, $P < 0.0001$. Residual home range sizes from Fig 3a. Partial regression plot, removing the variation explained by latitude.

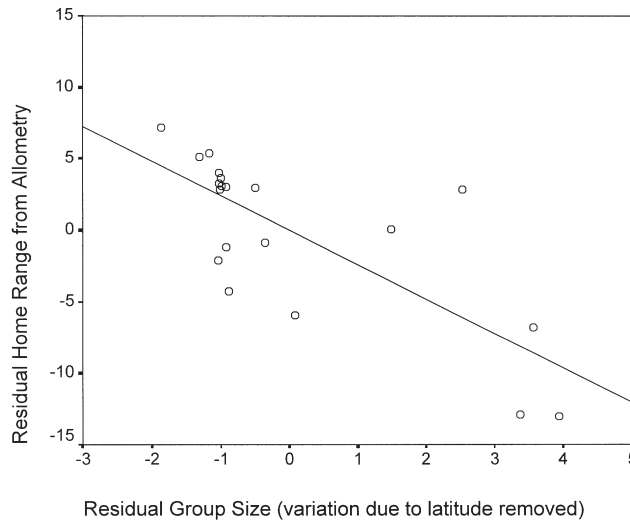
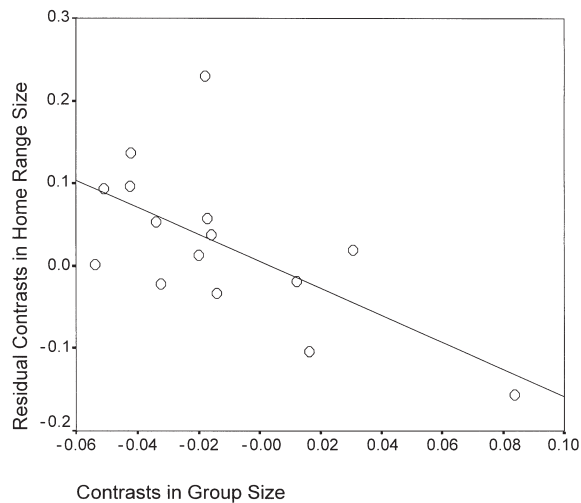


Fig. 5. Regression through the origin of contrasts in group size against residual contrasts in home range size using comparative analysis (CAIC). Partial regression, $r^2 = 0.51$, $t = -3.24$, $d.f. = 13$, $P < 0.01$, removing effects of female body mass.



area with increasing group size. This might occur because in many species' ranges, space is wasted or unused – a single animal may often have more than enough food. However, animals have long been argued to occupy minimum economically defensible areas (Brown, 1964), and Badgers, for example, are expected to seek to minimize their territories (Kruuk & Macdonald, 1985). Furthermore, none of the home range scaling studies (e.g. Swihart *et al.*, 1988; Kelt & Van Vuren, 1999) show any levelling off of home range size at the higher body masses, even when specifically controlled for group size (Gittleman & Harvey, 1982; Lindstedt *et al.*, 1986; Grant *et al.*, 1992). In addition, Harestad & Bunnell (1979) suggested that carnivore home ranges should increase disproportionately more steeply the larger the animal, because larger ranges are increasingly likely to contain redundant, unproductive habitat. Lindstedt *et al.* (1986) further argued that telemetry, which tends to overestimate home range, is more frequently used for larger carnivores and that many studies are biased

towards high latitudes, where low productivity means that carnivore home ranges are often unusually large.

All these arguments predict larger mustelids to have, if anything, larger home ranges than predicted by aM^k . We found the converse; social species, which are among the heaviest, have very much smaller home range sizes than expected by allometry. This is not a species-specific effect, because social populations of species that are non-social over most of their range (e.g. European Badgers and River Otters) have smaller home ranges than their solitary conspecifics.

Do resources determine sociality in mustelids?

The null model of allometry assumes similar resource availability among species. One hypothesis for the determinants of sociality is the Resource Dispersion Hypothesis (RDH; Kruuk, 1978b; Macdonald, 1983; Macdonald & Carr, 1989; Bacon, Ball & Blackwell, 1991a, b). This hypothesis would predict the observed lack of fit to an allometrically scaled home range size, as it holds that groups can form precisely because of non-random prey distribution (clumped in time or space). It does not expect any relationship between group size (or predator biomass) and home range size, and this has been demonstrated in several species thought to have dispersed or patchy resources, such as Badgers (Kruuk & Parish, 1982), Red Foxes *Vulpes vulpes* (Doncaster & Macdonald, 1992) and Black-backed Jackals *Canis mesomelas* and feral Cats *Felis catus* (Macdonald, 1983). Similarly, our inter-specific results also suggest that the social mustelids are sharing resources in some way. This is important for sociobiology, because the dispersion of resources can dictate social spacing (Von Schantz, 1984b), as well as mating systems directly (Powell, 1989; Davies, 1991). For example, Zabel & Taggart (1989) documented a switch from polygyny to monogamy in Red Foxes following climatic changes that led to an overall reduction in prey availability.

A further line of evidence supports the case for an ecological basis of social behaviour. Lindstedt *et al.* (1986) argued that an allometric exponent of 1.0 is expected, because an animal's metabolic requirements are not defined only over chronological time ($M^{0.75}$), but also over 'biological time'. The duration of 'virtually all' (Lindstedt *et al.*, 1986) physiological processes (e.g. muscle contraction time, digestion and life-span) scale allometrically as $M^{0.25}$. Thus, the sum of these ($M^{1.0}$) represents metabolic needs over biologically relevant time periods (Lindstedt *et al.*, 1986). Animals may therefore define their home range sizes according to critical biological periods. This fits a prediction of the RDH, that home ranges encompass patches that may be infrequently visited but are, at times, vital.

Support for this suggestion also comes from data on the European Badger in the UK, the Cape Clawless Otter *Aonyx capensis*, and the Shetland population of the European Otter (Kruuk, 1978b; Arden-Clarke, 1986; Kruuk & Moorhouse, 1991). At these sites, individual ranges overlap to form loose social groups in areas with dispersed feeding patches, all in situations reported as consistent with the RDH. We added data *posthoc* for the Cape Clawless Otter and both 'social' and 'non-social' populations of Badgers and Otters for comparison (denoted as 'x's) in Fig. 3(a).

If groups form because of patchy food distribution, then behavioural processes *per se* would not necessarily be a necessary explanatory variable of their sociality. An implication may be that such species exhibit an unusual mating system because local ecological variables have resulted in the presence of conspecifics. For example, Badgers in the UK prey on very abundant food and form groups with multiple paternity (Evans *et al.*, 1989). Other variables are likely to contribute but, apart from latitude, diet has been the only ecological factor shown to influence home range size in carnivores (Gittleman & Harvey, 1982) and small mammals (Mace, 1979).

Creel & Macdonald (1995) concluded from their analyses of the Carnivora that group size was largest in insectivores, followed by carnivores and omnivores, and then frugivores and herbivores. This also fits the above arguments and specifically one of the situations favouring sociality they describe (Creel & Macdonald, 1995), that because invertebrates are often locally abundant (e.g. Kruuk, 1978b) and rapidly renewing (e.g. Waser, 1981), species that prey on them can form social groups without great competition. However, among carnivores, insectivory may be constrained by body size (Carbone *et al.*, 1999), so effects of body size on sociality must first be ruled out. A further line of circumstantial support for an ecological basis of sociality comes from the observation that none of the social mustelids eat substantial numbers of small mammals, whereas nearly all of the others do. Perhaps, the limitation to a terrestrial meat diet, which is less abundant, less renewable and must therefore be defended, makes sociality unlikely. McNab (1995) showed that exclusively carnivorous mammals also had higher basal metabolic rates than those that mixed fruit and invertebrates in their diet (though $n = 8$), and this was independent of phylogeny. Sociality may even be unlikely between the two sexes of the same species; pronounced sexual dimorphism and intra-sexual territoriality may have emerged as a way of reducing food competition in the smaller mustelids. However, both sociality and non-sociality arise within species apparently eating the same food (e.g. European Otter in Shetland, Kruuk & Moorhouse, 1991; Badger in Britain & Norway, Hofer, 1988; Brøseth, Knutsen & Bevanger, 1997).

We expect some error for three reasons. Firstly, data collection methods and methods of home range size estimation vary (Swihart *et al.*, 1988). Secondly, an intra-sexual territorial system results in individuals of the opposite sex hunting in shared ranges, which means that home range size cannot be dependent on only a single individual's metabolic needs. Thirdly, resource distribution for aquatic predators is likely to be different, so comparing them directly with terrestrial carnivores may be of limited value. Nevertheless, the results support the notion that ecological factors, particularly food availability, do indeed underlie sociality in mustelids.

III. INTRA-SPECIFIC VARIATION IN SOCIAL ORGANIZATION

Our analyses of inter-specific variation and allometry have supported the hypothesis that local ecological conditions dictate animal density and spatial organization and hence determine social behaviour (e.g. Lindström, 1993; Bacon *et al.*, 1991b). In this section we investigate the evidence for this hypothesis deriving from variation within species. Numerous studies have reported extensive variation in social spacing patterns between study sites, years, social status and individuals, e.g. in American Badgers, Wolverines, North-American River Otters (all in Hornocker *et al.*, 1983; Reid *et al.*, 1994), Giant Otters (Carter & Rosas, 1997) and Stoats (Sandell, 1986), as well as variation in spacing patterns between the breeding and non-breeding season (Erlinge & Sandell, 1986). Creel & Macdonald (1995) cited several examples of carnivores formerly classified as solitary that sometimes exhibit some form of social grouping (e.g. Kruuk & Moorhouse, 1991) and there are specific examples of mating systems changing with resources over short time periods (Zabel & Taggart, 1989). Creel & Macdonald (1995) also quoted examples of species for which the conventional explanation of mating strategy is now known to be at least partly misleading because of sperm competition and extra-territorial mating (e.g. Ethiopian Wolf *Canis simensis*, Sillero-Zubiri, Gottelli & Macdonald, 1996; Badgers, Evans *et al.*, 1989). Many species are so poorly known that within-species variation would not yet have been identified and as more information accumulates about these species, classical models are often found not to apply. Furthermore, as habitat

alteration and climate change are altering the environment of many carnivores (Schaller, 1996), it seems likely that changes will be apparent in their density, spacing and sociobiology. In the following paragraphs, we examine the case of the European Badger in more detail in an attempt to identify what type of influences may account for intra-specific variation in their social organization.

In continental Europe, Badgers seem to be non-social, with mean group sizes of only one to three (Pigozzi, 1988; Woodroffe & Macdonald, 1993; Rodríguez *et al.*, 1996; Brøseth *et al.*, 1997; Revilla, 1998). However, in the UK, they commonly form large groups of up to 30 individuals that share a group territory and setts. One possible explanation for this great difference is that the mild and damp climate of the British Isles, with little snow cover and few dry periods, together with the high prevalence of pasture, provides ideal conditions for Earthworms *Lumbricus terrestris*, which are their principal prey (Kruuk, 1978a,b; Kruuk *et al.*, 1979; Kruuk & Parish, 1981, 1982; Ashby & Elliot, 1983; Hofer, 1988; Da Silva *et al.*, 1993; Roper, 1994). Such super-abundance could account for inflated densities of Badgers, which now find themselves sharing den sites in an unusually crowded social environment, different from the one in which they evolved (analogous to the social behaviour of feral Cats, Macdonald *et al.*, 1987). In continental Europe, Badgers have been found to specialize on very different foods, e.g. Rabbits *Oryctolagus cuniculus* in Spain (Martín, Rodríguez & Delibes, 1995) and insects and fruits in Italy (Pigozzi, 1987, 1988; Kruuk & De Kock, 1981).

Another (non-exclusive) explanation we have mentioned, the Resource Dispersion Hypothesis, could indicate why groups of Badgers occupy territories (Carr & Macdonald, 1986; Macdonald & Carr, 1989) and has support from modelling (Bacon *et al.*, 1991a,b). Groups may form where prey is unpredictably dispersed but locally abundant. Thus, conspecifics can share surpluses, but all have an individual stake in maintaining access to several patches, thereby leading to overlapping home ranges. They defend a similar space, creating a spatial group (Leyhausen, 1965; Macdonald, 1983; Carr & Macdonald, 1986), and may not gain any behavioural benefits from group living at all. Although groups of Badgers may exhibit some behaviourally important social interactions (Woodroffe, 1993; Stewart, Bonesi & Macdonald, 1999), there is no good evidence of any direct benefits of group living in this species (Woodroffe & Macdonald, 2000). If the social group is a result of individuals sharing dispersed resources, then this itself may be considered an explanation for their sociality. No behavioural explanations need be invoked.

The RDH predicts that territory size should generally be independent of group size, because an individual needs to defend the same number of patches, and thus guarantee food, as would a group (Kruuk & Macdonald, 1985); patches are available only with a constant mean rate and area. This is the case both within (e.g. Wytham, Oxfordshire, Johnson & Macdonald, unpublished data, $r_{21} = 0.188$, $P = 0.414$) and between (Kruuk & Parish, 1982; $r_{17} = -0.07$) UK populations. We tested this as a partial linear regression of home range size against group size across all populations studied across Europe and, after controlling for latitude, the relationship is still not significant (Fig. 6, $t = -1.86$, d.f. = 18, $P = 0.08$). There is, however, a negative trend. Either the RDH or a more general resource dependent explanation of social aggregation can be applied, in the absence of an alternative explanation (e.g. Doncaster & Woodroffe, 1993). Across Europe, Badger group sizes are large only where territories are small. Assuming similar body masses and energetic costs, only an increase in local resource richness can permit this. The most recent study (Feore & Montgomery, 1999) found no relationship between group size and territory size in Ireland, except in one habitat type, 'ideal Badger habitat' where food was 'readily available', in which a small increase in territory size allowed a proportionate increase in group membership. Whenever resources permit,

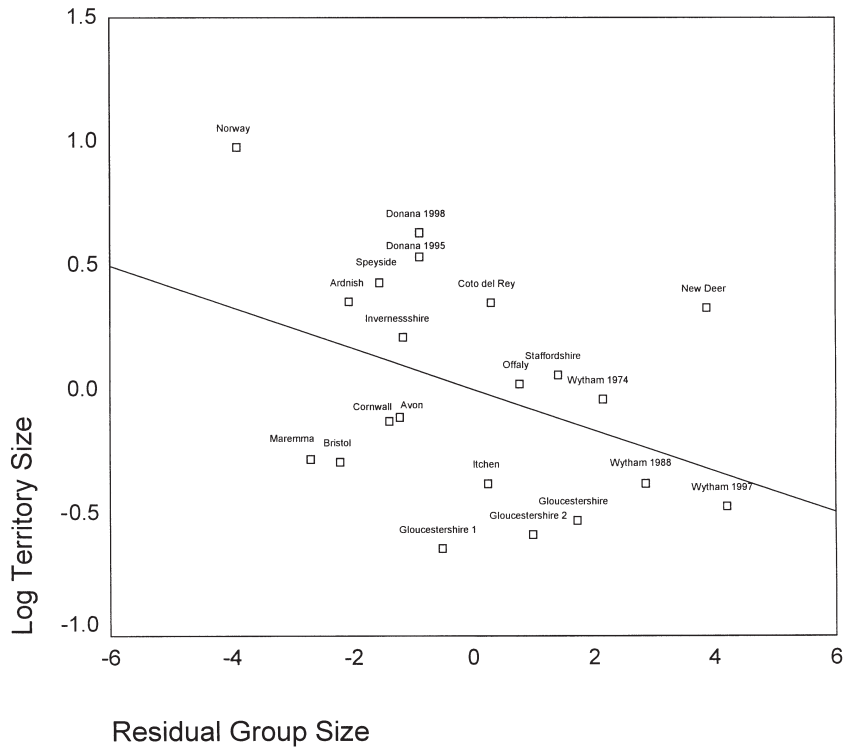


Fig. 6. Badger territory sizes against group sizes across Europe, controlling for latitude (Partial $t = -1.86$, d.f. = 18, $P = 0.08$). References are under number 40 in Appendix 2.

encourage or dictate the establishment of a group, there is potential for a consequent alteration in their sociobiological system (Alexander, 1974; Clutton-Brock & Harvey, 1978).

CONCLUSIONS

We set out to synthesize and evaluate hypotheses and data that might explain inter- and intra-specific variation in mustelid sociobiology. We have covered several seemingly separate areas of mustelid biology: an inter-specific analysis of life history variables, residuals of allometric home range scaling, and intra-specific variation in social organization. However, these all directly interact to mould social spacing patterns, which in turn dictate mating systems, and may complicate any unifying model of sociobiology for this family. The smaller mustelids, at least, tend to adhere to Powell's (1979) approximation of intra-sexual territoriality, but the sociobiology of the 'social' mustelids is completely different.

Our inter-specific analyses suggested two themes of sociobiology in the Mustelidae: (1) species that have evolved larger groups have simultaneously evolved tendencies towards fewer young per litter and possibly increased maternal investment, as there was a correlation between breeding group size and gestation*lactation. This is supported by the Principal Components Analysis in the high factor loadings for litter size and gestation period in PC 1. These results may imply that sociality tends to occur in animals with higher investment in fewer young. In contrast to these K-selected strategies, however, there was a negative relationship with longevity in the contrasts analysis. (2) The evolution of larger breeding group sizes in the mustelid phylogeny was associated with decreases, paradoxically, in group home

range size. This was a robust (and conservative) effect demonstrated in both raw species data and independent contrasts analyses of absolute home range controlling for female body mass, and when using group mass to control for biomass per unit area and residual home range size derived from allometric scaling. Similar trends in social and non-social populations of the same species offer further support that this phenomenon occurs intra-specifically as well. This demonstrates that social species have group home ranges very much smaller than expected from allometric, metabolic or latitudinal relationships. They are also among the heaviest species, yet we have quoted several lines of argument which show that home range area should, if anything, be disproportionately larger for heavy carnivores, not smaller, as we found.

One explanation for this is that they owe their unusual sociobiology to the patchy distribution of shareable food. In support of this idea, that it is simply the characteristics of the local environment that result in spatial groups (Leyhausen, 1965; Macdonald, 1983), the European Badger, Sea Otter and Giant Otter do not appear to obtain any benefits directly from functional aspects of group living *per se*, as do other social carnivores, such as alloparental care in African hunting dogs *Lycan pictus* (Frame *et al.*, 1979; Creel & Creel, 1991), defence of kills and co-operative hunting in hyaenas *Crocuta crocuta* (Mills, 1989) or coalition formation in lions *Panthera leo* (Bygott, Bertram & Hanby, 1979). We therefore tentatively suggest it is the particular dispersion of resources that allows or even dictates that these mustelids deviate from the solitary and territorial lifestyle otherwise descriptive of the family and order (Powell, 1979; Gittleman, 1989). Deviations from the Powell (1979) model might thus be constrained for the majority of other mustelids that eat small, slowly renewing prey (Macdonald, 1992), which bars the principal mechanism (Creel & Macdonald, 1995) through which social mustelids are argued to have attained sociality.

Previous reviews of social behaviour have classified mammalian mating systems into specific categories (Clutton-Brock, 1989; Davies, 1991; Ortolani & Caro, 1996). This is a necessary step for undertaking the sort of cross-species comparative analysis we have attempted. We do suggest, however, that it should not necessarily be expected that any species will fit an arbitrary classification higher than species level, because evolution leads to continuous variation and not to easily definable categories types, which are only a human convenience. This is even further supported by the evidence for wide intra-specific variation, which indicates that the classification of the mating system for a single species can be entirely study-dependent. These considerations favour the use of continuous dependent variables, such as breeding group size, instead of rather arbitrary ordinal or dichotomous classifications such as 'social' and 'non-social'. Analyses of the latter are definition-dependent, and therefore they are necessarily not objective.

A further problem for future studies is that explanations of life-history variables sought by comparative analyses may be irrelevant if ephemeral ecological influences can cause rapid behavioural plasticity which would operate on a time scale orders of magnitude faster than the adaptation of morphology and physiology.

Our inter-specific results should moreover be treated with caution because sample sizes were sometimes small, regressions of several variables were conducted, and one particular node may have driven some of the life-history correlations (because of the large size of the Giant Otter compared with its closest relatives). We believe, however, that these results provide some new insights into the long-standing debate on the causes of sociality, with the novel application of home range size allometry as a null model for studying ecological variation, a new data set and a recent phylogeny of the Carnivora.

Spatial groups, but particularly the truly social ones, will develop only if conspecifics tol-

erate each other, regardless of the mechanism for grouping. A caveat to the adaptive approach in searching for determinants of sociality comes from Balharry (1993), who suggested that although Pine Martens *Martes martes* occupy suitable environments for groups to form, they do not, because of a phylogenetic ('hard-wired') intolerance of conspecifics. Lindström's (1986) model specifically described how social groups can be maintained, principally through the retention of offspring, while resources permit, but in Balharry's (1993) study it appears that such a mechanism is obstructed, because immature animals are ousted regardless of resources. Urban areas are model RDH-type habitats, in which Red Foxes and Cats form groups (Harris, 1981; Macdonald, 1981; Macdonald *et al.*, 1987). A similar species to the Pine Marten, the Stone Marten *Martes foina*, also inhabits this habitat and eats similar foods, yet, in every study reviewed by Balharry (1993) they have maintained a rigid intra-sexual territoriality. Sexually mature young compete for mates and resources, so physiological and behavioural mechanisms have been selected to increase aggression towards offspring of dispersing age (Creel & Creel, 1991; Creel *et al.*, 1992). If this trait has evolved in some species as a 'hard-wired' behaviour, then in the medium-term it may override any cost-benefit trade-off in tolerance of conspecifics invoked in models of sociality (Macdonald & Carr, 1989). In many cases, such as that of the European Badger, we do not know which is the 'typical' spatial organization, so neither is it known to which social environment a species has predominantly been adapted.

Clearly, there is a great need for further explanation of the relatively wide variation in mustelid sociobiology. New methods for studies of paternity will prove invaluable in determining whether real paternity fits our initial assumptions about mating systems. There is also a need for an expansion of the criteria considered in potential explanations of life histories to include history and chance, as well as purely theoretical ideas such as optimality. Finally, we suggest there is much more to be done in at least ranking, if not quantifying, the potential underlying causes of social behaviour and group size variation in carnivores as a whole.

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APPENDIX 1

Data on mustelid life-history. References are in superscript numbers and are detailed in Appendix 2.

'Calc' = calculated from other data rows

Genus	species	Common Name	Breeding Group Size	Female Mass (kg)	Male Mass (kg)	Mean Adult Mass (kg)	Sexual Mass Ratio	Group Mass (kg)	Home Range (km ²)	Length of delay (days)	Gestation (days)
<i>Amblyonyx</i>	<i>cinereus</i>	Oriental Short-clawed Otter	12.00 ¹⁷	—	2.35 ¹⁰	—	—	—	—	0 ⁵⁰	62 ⁵⁰
<i>Aonyx</i>	<i>capensis</i>	Cape Clawless Otter	2.00 ⁸	18 ⁸	19.98 ^{calc}	18.99 ^{calc}	1.11 ⁸	36.00 ^{calc}	—	0 ⁵⁰	63 ⁸
<i>Aonyx</i>	<i>congius</i>	Zaire Clawless Otter	—	—	—	—	—	—	—	0 ¹⁷	60 ¹⁷
<i>Arctonyx</i>	<i>collaris</i>	Hog Badger	—	—	10.50 ¹⁶	—	—	—	—	—	42 ¹⁷
<i>Conepatus</i>	<i>chinga</i>	Hog-nosed Skunk	—	1.465 ¹⁰	2.37 ¹⁰	1.92 ^{calc}	1.62 ^{calc}	—	—	—	—
<i>Conepatus</i>	<i>humboldtii</i>	Patagonian Skunk	1.00 ³²	1.323 ³²	—	—	—	1.32 ^{calc}	1.64 ³²	—	—
<i>Conepatus</i>	<i>leuconotus</i>	Eastern Hog-nosed Skunk	—	—	—	—	—	—	—	—	—
<i>Conepatus</i>	<i>mesoleucus</i>	Western Hog-nosed Skunk	1.00 ¹⁷	2.13 ³²	1.89 ³²	2.01 ^{calc}	—	2.13 ^{calc}	—	60 ¹⁶	42 ¹⁶
<i>Conepatus</i>	<i>semistriatus</i>	Amazonian Skunk	—	—	—	—	—	—	—	—	—
<i>Eira</i>	<i>barbara</i>	Tayra	1.00 ⁸	4.4 ⁸	4.84 ^{calc}	4.62 ^{calc}	1.10 ⁸	4.40 ^{calc}	—	0 ⁵⁰	64 ⁸
<i>Enhydra</i>	<i>lutris</i>	Sea Otter	6.00 ⁸	19.9 ⁸	27.66 ^{calc}	23.78 ^{calc}	1.39 ⁸	119.40 ^{calc}	2.50 ⁸	130 ¹²	65 ⁸
<i>Galictis</i>	<i>cuja</i>	Little Grison	—	1 ¹⁷	1.00 ¹⁶	1.00 ^{calc}	—	—	—	—	—
<i>Galictis</i>	<i>vittata</i>	Grison	—	1.8 ⁸	3.38 ^{calc}	2.59 ^{calc}	1.88 ⁸	—	—	—	—
<i>Gulo</i>	<i>gulo</i>	Wolverine	1.00 ⁸	10.6 ⁵	14.80 ⁵	12.70 ^{calc}	1.30 ⁵	10.60 ^{calc}	405.00 ⁸	195 ¹²	35 ⁸
<i>Ictonyx</i>	<i>libyca</i>	North African Banded Weasel	1.00 ⁸	—	0.23 ¹⁷	—	—	—	—	0 ⁵⁰	55 ¹⁷
<i>Ictonyx</i>	<i>striatus</i>	Zorilla	1.00 ⁸	1.3 ⁸	1.87 ^{calc}	1.59 ^{calc}	1.44 ⁸	1.30 ^{calc}	—	0 ⁵⁰	36 ¹⁵
<i>Lontra</i>	<i>canadensis</i>	North American River Otter	1.00 ³	7.8 ⁸	8.58 ^{calc}	8.19 ^{calc}	1.10 ⁸	31.20 ^{calc}	36.65 ^{2,55}	240 ²	62 ²
<i>Lontra</i>	<i>felina</i>	Marine Otter	1.00 ³⁹	4 ³⁹	4.00 ³⁹	4.00 ^{calc}	1.00 ³³	4.00 ^{calc}	—	—	65 ¹⁶
<i>Lontra</i>	<i>longicaudis</i>	Neotropical River Otter	—	3.86 ¹⁰	9.25 ¹⁰	6.56 ^{calc}	2.40 ^{calc}	—	—	—	—
<i>Lontra</i>	<i>provocax</i>	Southern River Otter	—	—	—	—	—	—	—	—	—
<i>Lutra</i>	<i>lutra</i>	European River Otter	3.50 ⁸	5.2 ⁸	9.00 ^{calc}	7.10 ^{calc}	1.73 ⁸	18.20 ^{calc}	29.20 ⁸	0 ⁵⁰	62 ⁸
<i>Lutra</i>	<i>maculicollis</i>	Spot-necked Otter	4.50 ⁸	3.5 ⁸	4.38 ^{calc}	3.94 ^{calc}	1.25 ⁸	15.75 ^{calc}	—	0 ¹³	56 ⁸
<i>Lutra</i>	<i>sumatrana</i>	Hairy-nosed Otter	—	—	—	—	—	—	—	—	—
<i>Lutrogale</i>	<i>perspicillata</i>	Indian Smooth-coated Otter	2.00 ⁸	7.3 ⁸	10.29 ^{calc}	8.80 ^{calc}	1.41 ⁸	14.60 ^{calc}	7.00 ⁸	0 ⁵⁰	62 ⁸
<i>Lyncodon</i>	<i>patagonicus</i>	Patagonian Weasel	—	—	—	—	—	—	—	—	—
<i>Martes</i>	<i>americana</i>	American Marten	1.00 ⁸	0.77 ⁸	0.97 ^{calc}	0.87 ^{calc}	1.26 ⁸	0.77 ^{calc}	1.60 ⁸	225 ¹²	27 ⁸
<i>Martes</i>	<i>flavigula</i>	Yellow-throated Marten	3.00 ¹⁷	3.4 ¹⁰	—	—	—	10.20 ^{calc}	—	105 ¹⁶	60 ¹⁶
<i>Martes</i>	<i>foina</i>	Stone Marten	1.00 ¹⁶	1.45 ¹⁴	1.83 ¹⁴	1.64 ^{calc}	1.26 ^{calc}	1.45 ^{calc}	3.61 ²⁴	240 ³⁸	30 ³⁸
<i>Martes</i>	<i>gwatkinsii</i>	Nilgiri Marten	—	—	—	—	—	—	—	—	45 ¹⁶
<i>Martes</i>	<i>martes</i>	Pine Marten	1.50 ⁸	1.2 ⁸	1.20 ^{calc}	1.20 ^{calc}	1.00 ⁸	1.80 ^{calc}	1.50 ⁸	210 ¹⁶	30 ⁸
<i>Martes</i>	<i>melampus</i>	Japanese Marten	1.00 ¹⁶	—	—	—	—	—	—	195 ¹⁶	45 ¹⁶
<i>Martes</i>	<i>pennanti</i>	Fisher	1.00 ⁸	2.25 ⁷	4.50 ⁷	3.38 ^{calc}	2.00 ⁸	2.25 ^{calc}	15.00 ⁷	315 ⁷	30 ⁷
<i>Martes</i>	<i>zibellina</i>	Sable	1.00 ⁸	1.03 ⁸	1.35 ^{calc}	1.19 ^{calc}	1.31 ⁸	1.03 ^{calc}	—	247 ¹⁷	28 ⁸
<i>Meles</i>	<i>meles</i>	European Badger	4.65 ⁴⁰	10.9 ⁸	12.32 ^{calc}	11.61 ^{calc}	1.13 ⁸	50.69 ^{calc}	1.73 ^{40,a}	255 ¹²	42 ⁸
<i>Mellivora</i>	<i>capensis</i>	Honey Badger	1.70 ⁸	7.59 ⁸	8.58 ^{calc}	8.08 ^{calc}	1.13 ⁸	12.90 ^{calc}	—	—	—
<i>Melogale</i>	<i>everetti</i>	Indian Ferret Badger	—	—	2.00 ¹⁶	—	—	—	—	—	—
<i>Melogale</i>	<i>moschata</i>	Chinese Ferret Badger	—	—	2.00 ¹⁶	—	—	—	—	—	—
<i>Melogale</i>	<i>orientalis</i>	Oriental Ferret Badger	—	—	2.00 ¹⁶	—	—	—	—	—	—
<i>Mephitis</i>	<i>macroura</i>	Hooded Skunk	—	0.717 ¹⁰	0.89 ¹⁰	0.80 ^{calc}	1.24 ^{calc}	—	—	30 ¹⁶	63 ¹⁶
<i>Mephitis</i>	<i>mephitis</i>	Striped Skunk	4.60 ⁸	2 ⁸	2.80 ^{calc}	2.40 ^{calc}	1.40 ⁸	9.20 ^{calc}	4.50 ⁸	30 ¹⁶	68 ⁶
<i>Mustela</i>	<i>africana</i>	Tropical Weasel	—	—	—	—	—	—	—	—	—
<i>Mustela</i>	<i>altaica</i>	Mountain Weasel	1.00 ⁸	0.13 ⁸	0.25 ^{calc}	0.19 ^{calc}	1.92 ⁸	0.13 ^{calc}	—	0 ⁵⁰	40 ⁸
<i>Mustela</i>	<i>erminea</i>	Stoat/Ermine	1.00 ⁸	0.13 ⁸	0.23 ^{calc}	0.18 ^{calc}	1.77 ⁸	0.13 ^{calc}	0.10 ⁸	270 ¹²	35 ⁸
<i>Mustela</i>	<i>eversmannii</i>	Steppe polecat	1.00 ¹⁶	1.35 ¹⁷	2.05 ¹⁷	1.70 ^{calc}	1.52 ^{calc}	1.35 ^{calc}	—	0 ⁵⁰	41 ³⁰
<i>Mustela</i>	<i>felipei</i>	Colombian weasel ⁸	—	—	—	—	—	—	—	—	—
<i>Mustela</i>	<i>frenata</i>	Long-tailed Weasel	1.00 ³	0.165 ³	0.31 ³	0.24 ^{calc}	1.85 ³	0.17 ^{calc}	0.17 ³	183 ³	27 ³
<i>Mustela</i>	<i>kathiah</i>	Yellow-bellied Weasel	—	0.201 ¹⁰	0.36 ¹⁰	0.28 ^{calc}	1.79 ^{calc}	—	—	—	—
<i>Mustela</i>	<i>lutreola</i>	European Mink	1.00 ⁸	0.44 ⁸	0.74 ^{calc}	0.59 ^{calc}	1.68 ⁸	0.44 ^{calc}	0.18 ¹⁷	8.5 ^{17,c}	30 ⁸
<i>Mustela</i>	<i>lutreolina</i>	Indonesian Mountain Weasel	1.00 ¹⁷	—	0.62 ¹⁰	—	—	—	—	—	—
<i>Mustela</i>	<i>nigripes</i>	Black-footed Ferret	1.00 ¹⁷	0.809 ¹⁷	1.02 ¹⁷	0.92 ^{calc}	1.26 ^{calc}	0.81 ^{calc}	—	0 ¹²	42 ³⁰
<i>Mustela</i>	<i>nivalis</i>	European Common Weasel	1.00 ⁸	0.06 ⁸	0.10 ^{calc}	0.08 ^{calc}	1.67 ⁸	0.06 ^{calc}	0.12 ⁸	0 ⁴⁵	36 ⁸
<i>Mustela</i>	<i>nudipes</i>	Barefoot Weasel	—	—	—	—	—	—	—	—	—
<i>Mustela</i>	<i>putorius</i>	European polecat	1.00 ⁸	0.8 ⁸	1.26 ^{calc}	1.03 ^{calc}	1.58 ^{calc}	0.80 ^{calc}	13.00 ⁸	0 ¹²	41 ⁸
<i>Mustela</i>	<i>sibirica</i>	Kolinsky	1.00 ⁸	0.4 ⁸	0.74 ^{calc}	0.57 ^{calc}	1.85 ⁸	0.40 ^{calc}	—	0 ⁵⁰	29 ⁸
<i>Mustela</i>	<i>strigidorsa</i>	Back-striped Weasel	—	—	—	—	—	—	—	—	—
<i>Mustela</i>	<i>vison</i>	American Mink	1.00 ⁸	0.61 ⁸	1.21 ^{calc}	0.91 ^{calc}	1.98 ⁸	0.61 ^{calc}	1.90 ⁸	18.5 ⁴⁵	29 ⁸
<i>Mydaus</i>	<i>javanensis</i>	Teledu/Sunda Stink Badger	—	—	2.60 ¹⁶	—	—	—	—	—	—
<i>Mydaus</i>	<i>marchei</i>	Palawan Stink Badger	—	—	3.00 ¹⁶	—	—	—	—	—	—
<i>Poecilogale</i>	<i>albinucha</i>	African Striped Weasel	1.00 ⁸	0.34 ⁸	0.50 ^{calc}	0.42 ^{calc}	1.48 ⁸	0.34 ^{calc}	—	0 ⁵⁰	32 ⁸
<i>Pteronura</i>	<i>brasiliensis</i>	Giant Otter	6.00 ²²	24 ¹⁰	26.00 ¹⁰	25.00 ^{calc}	1.08 ^{calc}	144.00 ^{calc}	5.00 ^{22,a}	0 ⁵⁰	61 ²²
<i>Spilogale</i>	<i>putorius</i>	Eastern Spotted Skunk	1.00 ¹⁶	0.283 ⁴	0.40 ⁴	0.34 ^{calc}	1.41 ⁴	0.28 ^{calc}	—	0 ⁴	57.5 ⁴
<i>Spilogale</i>	<i>pygmaea</i>	Pygmy Spotted Skunk	1.00 ¹	0.23 ¹⁰	0.50 ¹⁶	0.37 ^{calc}	2.17 ^{calc}	0.23 ^{calc}	—	0 ⁵⁰	47 ¹
<i>Taxidea</i>	<i>taxus</i>	American Badger	1.20 ⁸	6.3 ⁸	6.30 ^{calc}	6.30 ^{calc}	1.00 ⁸	7.56 ^{calc}	5.40 ⁸	195 ¹²	42 ⁸
<i>Vormela</i>	<i>peregrina</i>	Marbled Polecat	1.00 ¹⁷	0.53 ⁸	0.67 ^{calc}	0.60 ^{calc}	1.26 ⁸	0.53 ^{calc}	—	223 ^b	62 ⁸

a-Group Territory

b-Calculated from ref. 21 minus true gestation from ref. 8

c-Some females show a short and variable period of delayed implantation

Litters per year	Litter Size	Lactation Period (days)	Months to Sexual maturity	Longevity** (months)	Ovulation Type	Seasonal Breeding	Social Class****	> 60% Carnivory	Diet Class	Delayed implantation
1.5 ¹⁷	3.5 ¹⁶	80 ¹⁷	—	—	—	Yes ⁵⁰	4 ¹⁷	—	Omnivorous ⁵³	No ⁵⁰
1 ¹⁷	3.0 ⁸	63 ⁸	—	132 ¹⁷	—	Yes ⁵⁰	2 ⁸	No ⁸	Other Invertebrates ⁹	No ⁵⁰
—	2.5 ¹⁷	—	12 ¹⁷	—	—	—	3 ⁴⁶	—	No ¹⁷	—
1 ⁵⁰	3.0 ¹⁷	—	—	167 ¹⁷	—	Yes ¹²	—	—	Yes ¹²	—
1 ¹⁷	—	—	—	79 ¹⁷	—	—	—	—	Insectivorous ²⁰	—
—	—	—	—	—	—	—	1 ³²	—	Yes ²⁰	—
—	—	—	—	—	—	—	—	—	Yes ²⁰	—
1 ⁵⁰	3.0 ¹⁶	—	—	—	—	Yes ⁵⁰	1 ¹⁷	—	Yes ²⁰	—
—	—	—	—	—	—	—	—	—	Yes ²⁰	—
1 ¹⁷	3.5 ⁸	—	—	144 ⁸	—	Yes ⁵⁰	1 ⁴⁶	No ⁸	Insectivorous ²⁰	—
1 ³⁵	1.0 ⁸	65 ⁸	36.5 ¹⁵	228 ¹⁷	—	Yes ¹²	3 ⁴⁶	Yes ⁸	Carnivorous ⁴²	No ⁵⁰
—	—	—	—	—	—	—	3 ¹⁷	—	—	—
—	2.0 ⁸	—	—	126 ¹⁷	—	—	3 ¹⁷	Yes ⁸	Carnivorous ⁴²	—
1 ⁵	2.8 ⁸	70 ⁸	21 ¹⁵	186 ⁸	Induced ²⁸	Yes ⁵⁰	1 ⁸	Yes ⁸	Carnivorous ¹⁸	Yes ¹²
1 ¹⁷	2.5 ¹⁷	—	—	60 ¹⁷	—	Yes ¹³	1 ⁸	—	No ⁵⁰	—
1 ¹⁷	2.3 ⁸	56 ⁸	9 ⁹	60 ⁸	—	Yes ⁵⁰	1 ⁸	No ⁸	Omnivorous ¹³	No ⁵⁰
1 ¹⁶	3.0 ⁸	84 ²	30 ¹⁷	156 ²	Induced ²	Yes ²	3 ²	Yes ⁸	Piscivorous ²	Yes ²
—	2.0 ¹⁶	—	—	—	—	Yes ³³	1 ³³	Yes ³³	Piscivorous ⁴⁸	—
—	2.5 ¹⁶	—	—	—	—	Yes ¹⁶	—	—	—	—
—	—	—	—	—	—	—	—	Yes ¹⁷	Other Invertebrates ³⁴	—
—	2.5 ⁸	112 ⁸	30.4 ¹⁵	49 ⁸	—	Yes ⁵⁰	3 ⁸	Yes ⁸	Piscivorous ⁴⁹	No ⁵⁰
1 ⁵⁰	1.5 ⁸	—	—	—	—	Yes ¹⁶	3 ⁸	Yes ⁸	Piscivorous ¹³	No ⁵⁰
—	—	—	—	—	—	—	—	—	—	—
1 ⁵⁰	1.5 ¹⁵	126 ⁸	24.3 ¹⁵	180 ⁸	—	Yes ¹⁶	2 ⁸	Yes ⁸	—	No ⁵⁰
—	—	—	—	—	—	—	—	—	—	—
1 ¹⁷	2.6 ⁸	46 ⁸	12 ¹⁵	150 ⁸	—	Yes ¹²	1 ⁸	Yes ⁸	—	Yes ¹²
1 ¹⁶	2.5 ¹⁷	—	—	168 ¹⁷	—	Yes ¹²	3 ¹⁷	—	Yes ¹²	—
1 ¹⁶	3.5 ¹⁷	—	—	217 ¹⁷	—	Yes ¹²	1 ¹⁶	No ²⁶	—	Yes ³⁸
1 ¹⁶	3.0 ¹⁶	—	—	—	—	—	1 ¹⁶	—	Yes ¹²	—
1 ¹⁷	3.3 ⁸	45 ¹⁷	24 ¹⁷	204 ¹⁷	—	Yes ¹²	1 ⁸	Yes ⁸	Carnivorous ⁴³	Yes ¹³
1 ¹⁶	3.0 ¹⁶	—	—	—	—	—	1 ¹⁶	No ²⁷	Omnivorous ²⁷	Yes ⁵⁰
1 ¹⁷	3 ⁷	63 ⁷	12 ⁷	120 ⁷	—	Yes ¹²	1 ⁷	Yes ⁸	Carnivorous ⁷	Yes ⁷
1 ¹⁶	3.0 ⁸	49 ⁸	20 ¹⁵	180 ¹⁷	Induced ²⁸	Yes ¹²	1 ⁸	No ⁸	—	Yes ⁵⁰
1 ¹⁷	3.0 ⁸	95 ⁸	17.5 ¹⁵	180 ⁸	—	Yes ¹²	3 ⁸	No ⁸	Insectivorous ¹³	Yes ¹²
1 ¹⁶	2.5 ⁸	—	—	288 ⁸	—	—	2 ⁸	No ⁸	Insectivorous ¹³	Yes ⁵⁰
—	2.0 ¹⁷	—	—	—	—	—	—	—	—	—
—	2.0 ¹⁷	—	—	—	—	—	—	—	—	—
—	2.0 ¹⁷	—	—	—	—	—	—	No ²³	Insectivorous ²³	—
1 ¹⁶	4.0 ¹⁶	—	—	—	—	Yes ¹⁶	1 ¹⁶	—	Yes ¹⁶	—
1 ¹⁶	6.8 ⁶	56 ⁶	10.3 ¹⁵	120 ⁶	Induced ⁶	Yes ⁶	3 ⁸	No ⁸	Insectivorous ⁶	Yes ¹⁶
—	—	—	—	—	—	—	—	—	—	—
1 ¹⁷	4.0 ⁸	56 ⁸	—	—	—	Yes ⁵⁰	1 ⁸	Yes ⁸	—	No ⁵⁰
1 ¹⁷	4.5 ⁸	63 ⁸	2.5 ^{17*}	18 ³⁶	Induced ⁵⁷	Yes ¹²	1 ⁸	Yes ⁸	Carnivorous ⁴³	Yes ¹²
1 ³⁰	6.9 ²⁹	45 ¹⁷	9 ¹⁷	—	—	Yes ⁵⁰	1 ¹⁶	Yes ⁵⁶	Carnivorous ⁵⁶	No ⁵⁰
—	—	—	—	—	—	—	—	—	—	—
1 ³	4.5 ³	35 ³	8.4 ¹⁵	—	Induced ⁵⁴	Yes ³	1 ³	Yes ³	—	Yes ³
—	—	—	—	—	—	—	—	Yes ¹⁷	—	—
1 ¹⁷	4.5 ⁸	70 ⁸	12 ¹⁵	120 ¹⁷	Induced ²⁸	Yes ¹³	1 ⁸	Yes ⁸	—	Yes ¹⁷
—	—	—	—	—	—	—	1 ¹⁷	—	—	—
1 ³⁰	3.5 ¹⁷	—	—	144 ¹⁷	—	Yes ¹³	1 ¹⁷	Yes ¹⁷	—	No ¹²
1.5 ³³	5.8 ⁸	32 ⁸	4.0 ¹⁷	10.56 ^{***59}	—	Yes ³³	1 ⁸	Yes ⁸	Carnivorous ⁴³	No ⁴⁵
—	4.0 ¹⁷	—	—	—	—	—	—	—	—	—
1 ¹⁷	6.0 ⁸	—	24 ³²	72 ¹⁷	Induced ⁴¹	Yes ⁴¹	1 ⁸	Yes ⁸	—	No ¹²
1 ¹⁷	5.0 ⁸	56 ⁸	—	106 ¹⁷	—	Yes ¹³	1 ⁸	Yes ⁸	—	No ⁵⁰
—	—	—	—	—	—	—	—	—	—	—
1 ¹⁷	5.0 ⁸	63 ⁸	14 ¹⁵	120 ¹⁷	Induced ²⁸	Yes ¹²	1 ¹⁸	Yes ⁸	Carnivorous ⁶⁵	Yes ⁵²
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
1 ¹⁸	2.0 ⁸	77 ⁸	18 ¹⁷	62 ¹⁷	—	Yes ¹³	1 ¹⁷	Yes ⁸	Carnivorous ⁹	No ⁵⁰
0.5 ²²	2.0 ²²	270 ²²	24 ²²	154 ¹⁷	—	No ²²	4 ²²	Yes ²²	Piscivorous ²²	No ⁵⁰
1 ¹⁶	5.5 ⁴	54 ⁴	—	118 ¹⁷	Spontaneous ⁴	Yes ⁴	3 ⁴	No ⁸	—	No ⁴
1.5 ¹	3.5 ¹	54 ¹⁷	—	118 ¹⁷	—	Yes ¹	1 ¹	No ¹	Omnivorous ¹	No ⁵⁰
1 ¹⁷	4.0 ⁸	42 ⁸	13.2 ¹⁵	156 ⁸	—	Yes ¹²	1 ⁸	Yes ⁵⁰	—	Yes ¹²
1 ¹⁷	6.0 ⁸	—	—	107 ¹⁷	—	Yes ¹⁶	1 ¹⁶	No ⁸	—	Yes ⁵⁰

*Sexual maturity in stoats is unusual: females conceive at 5-8 weeks; males reach sexual maturity at ~1 year (King, 1984; King & Moody, 1982)

**Longevity is data from a mixture of captive and wild animals

*** Data from animals killed in traps

**** Social class: (1) solitary, (2) pairs, (3) variable groups and (4) groups

APPENDIX 2

References for sources of mustelid data in Appendix 1.

- | | | | |
|----|--------------------------------------|----|--|
| 1 | Medellín, Ceballos & Zarza (1998) | 35 | Riedman <i>et al.</i> (1994) |
| 2 | Larivière & Walton (1998) | 36 | Sandell (1984) |
| 3 | Sheffield & Thomas (1997) | 37 | Hornocker <i>et al.</i> , 1983 |
| 4 | Kinlaw (1995) | 38 | Canivenc & Bonnin (1981) |
| 5 | Pasitschniak-Arts & Larivière (1995) | 39 | Larivière (1998) |
| 6 | Wade-Smith & Verts (1982) | 40 | Combined: Kruuk & Parish (1982, 1987); Kruuk <i>et al.</i> (1979), Cheeseman <i>et al.</i> (1981, 1985); Harris (1982); Harris & Cresswell (1987); Johnson & Macdonald, unpublished data; O'Corry-Crowe <i>et al.</i> (1993); Packham (1983); Hofer, 1988; Rodriguez <i>et al.</i> (1996); Revilla (1998); Woodroffe & Macdonald (1993); Brøseth <i>et al.</i> (1997). |
| 7 | Powell (1981) | 41 | Blandford (1987) |
| 8 | Creel & Macdonald, 1995 | 42 | Bisbal (1986) |
| 9 | Kingdon (1997) | 43 | Dayan & Simberloff (1994) |
| 10 | Silva & Downing (1995) | 45 | Mead (1981) |
| 11 | Macdonald, 1992 | 46 | Ortolani & Caro (1996) |
| 12 | Sandell (1990) | 47 | Estes (1989) |
| 13 | Gittleman, 1989 | 48 | Ebensperger & Botto-Mahan (1987) |
| 14 | Sandell, 1989 | 49 | Taastrøm & Jacobsen (1999) |
| 15 | Gittleman, 1986 | 50 | Mead (1989) |
| 16 | Macdonald (1984) | 51 | Dunstone (1993) |
| 17 | Nowak & Paradiso (1983) | 52 | Murphy <i>et al.</i> (1990) |
| 18 | Moors, 1980 | 53 | Mason & Macdonald (1986) |
| 19 | Alterio (1998) | 54 | King (1989b) |
| 20 | Travaini <i>et al.</i> (1998) | 55 | Foy 1984, cited in Larivière & Walton (1998) |
| 21 | Ben-David (1998) | 56 | Macdonald & Barrett (1993) |
| 22 | Carter & Rosas, 1997 | 57 | Macdonald (1995) |
| 23 | Chuang & Lee (1997) | 58 | Izor & de la Tóree (1978) |
| 24 | Genovesi <i>et al.</i> (1997) | 59 | King (1980) |
| 25 | Schröpfer <i>et al.</i> , 1997 | | |
| 26 | Genovesi <i>et al.</i> (1996) | | |
| 27 | Tatara & Doi (1994) | | |
| 28 | Mead <i>et al.</i> (1991) | | |
| 29 | Mead & Neirinckx (1990) | | |
| 30 | Mead, Neirinckx & Czekala (1990) | | |
| 31 | Clark <i>et al.</i> (1989) | | |
| 32 | Fuller <i>et al.</i> (1987) | | |
| 33 | Jedrzejewska (1987) | | |
| 34 | Medina (1997) | | |