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Mating system and genetic variance in a polygynous mustelid, the European polecat

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The population genetic implications of mating system were investigated in European polecat *Mustela putorius* populations from western France, combining radiotracking survey and allozyme variation analysis. Mating period occurred from February to June and polecats showed a strategy of successive polygyny, a male consorting with 1.44 females during a brief period (2.9 days). Relatedness was largely sex biased, females (21%) being almost twice more related than males (13%) suggesting a natal philopatry. Nonetheless, breeding dispersal pattern appeared relatively complex. Males were the sex dispersing but the main strategy for male polecats consisted of short-term mating excursions in adjacent females ranges whereas long-distance dispersal only constituted an alternative breeding strategy. Despite their allozymic polymorphism level reaching 24% at $p<0.05$ for 38 scored loci, populations showed a high heterozygote deficiency as revealed by the F_{IS} index averaging $F_{IS} = 0.383$. Thus the mating system of such solitary mustelids may be poorly efficient to prevent inbreeding within populations.

INTRODUCTION

The sexual system has a major influence on the genetic structure of wildlife populations. Monogamy is expected to retain high genetic diversity by allowing an equivalent share of reproduction among animals. Far from being panmictic, numerous social species are however structured into small breeding units that are susceptible to amplify inbreeding. Thus, a family effect can affect the genetic structure of social species living either in packs, such as wolves (Kennedy et al., 1991; Randi et al., 1993; Forbes and Boyd, 1996), or in small colonies, such as badgers or mongooses (Evans et al., 1989; Keane et al., 1996; Vuuren and Robinson, 1997). Similarly, polygyny may increase inbreeding by reducing the effective number (*Ne)* of breeders.

Nevertheless, most of mammals are polygynous species showing a male-biased dispersion (Greenwood 1980) and the design proves to be quite efficient in reducing the heterozygote deficit especially when populations are evenly distributed (Gotelli et al., 1994; Keane et al., 1996). Although dispersal may be costly, such a sex-biased strategy may generally favour the inbreeding avoidance. Polygyny however occurs in various patterns: there are social groups with a single dominant male as well as rather solitary animals mating with several females. Close inbreeding is rare in wild carnivores living in polygynous or promiscuous social groups mainly because social dominance and dispersal may proceed as a mechanism of inbreeding avoidance (Frame et al., 1979; Packer and Pusey, 1993; Smale et al., 1993; Woodroffe et al., 1995; Keane et al., 1996). Besides, intraspecific variations in mating systems frequently exist within sexes

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(Zabel and Taggart, 1989; Thirgood, 1990; Herrera and MacDonald, 1993; Gompper et al., 1997) and these alternative strategies may play a part in inbreeding avoidance and heterozygote depletion or excess (Rood, 1989). Although most solitary carnivores are portrayed as polygynous species, such mechanisms of inbreeding avoidance are still poorly known.

In polygynous species, sexual selection has also resulted in sexual dimorphism for size (Ralls, 1977). Conferring a sexual advantage by being large, sexual dimorphism in males is expected to occur when males compete for mate inducing a male-biased dispersion. Subordinate males are expected to be poor competitors, thus leaving their natal range might benefit from better opportunities to acquire matings. The polecat displays the strongest sexual dimorphism among mustelids and this dimorphism may be attributed to a strong mating competition among males (Poole, 1974). Indeed, the polecat has very individualistic habits exhibiting a strong segregation in the habitat use within or even between sexes (Lodé, 1996; 2000). Although polecats are expected to compete for females, little information is known about the factors that affect male and female mating patterns. It could be predicted that male conflicts result in a polygynous mating system with long distance dispersal, thus favouring inbreeding avoidance while females could rather show natal philopatry.

Using a combination of allozymic data and radiotracking survey of several polecats, this paper aims to 1) investigate the mating system as revealed by consortship behaviour and 2) analyse the genetic consequences of the mating system regarding genetic variance, relatedness and inbreeding.

MATERIALS AND METHODS

Mating system. Data from 22 reproductive adult polecats (9 males and 13 females) inhabiting western France were used to analyse mating behaviour from 1992 to 1999. During every surveyed period, trapping sessions were monthly conducted using 20 box-traps in four distinct areas: 1) Grand-Lieu, swampy meadows alternating with deciduous woods, 2) Brière, marshes and peat-bogs, 3) Brittany riverbank sides and farmland, 4) Anjou: deciduous woods (DPN authorisation n° 94162/AUT). The range of mean daily temperature was moderate (February: 2°C, August:21°C) and rainfall reached 750mm per year with less than three snowy days. Wild polecats were live-trapped, sexed, weighed, and their ano-genital region was meticulously examined. Polecats are monoestrous and animals are mature in the year following their birth (Lodé, 1990; Birks and Kitchener, 1999). The duration of the breeding period and dates of parturition were assessed on the basis of change in morphological external characteristics, testes, vulva and teats.

Mating behaviour was determined by three lines of evidence: trapping, incidental observations and radiotracking locations. Radiotracked polecats were repeatedly monitored by triangulation (Cf Lodé, 1994; 1995; 2000). The size of the activity area was calculated from the minimum convex polygon (Mohr, 1947; White and Garott, 1990). Nevertheless, only few data were obtained from one male and four females because of dysfunction or loss of their transmitter and their data were excluded from the estimation of home-range size. A limitation of the fieldwork is that the presence of transient polecats may not be detected despite they have a mating activity. Such a case is however expected to be rare because polecats showed a strong intolerance against congeners (Poole, 1974; Lodé, 1996).

The mating behaviour was inferred from data obtained by the radio-telemetry protocol considering the minimal consortship duration. The consortship behaviour consists in a brief diurnal association between an adult male and an adult female often resting together in the same den during oestrus (Gehrt and Fritzell, 1999). Polecats are usually intolerant and exhibit a strong individual segregation in the use of space and associations between individuals are restricted to the breeding period (Lodé, 1996). Most of recaptured females during this period exhibited scratches on the neck and on the back resulting from the copulation, when the male kept on the female with a bite often lasting more than one hour (Lodé, 1990). Because copulation induces ovulation, breeding success depends upon the male tenacity. Because of the nocturnal habits of polecats (Lodé, 1995), mating can only be indirectly evidenced by the consortship of male and female. Therefore, the consortship behaviour provides a good indication of the mating activity (Gehrt and Fritzell, 1999). The minimal consortship duration was assessed as a number of days during which male and female were diurnally associated in the den. I quantified the number of females consorted with each male and the time spent consorting was assessed considering successive locations on a basis of a minimum of six consecutive fixes per days.

Allozyme analysis. Polecats were sampled between 1996 and 1999 from six regions of western France, Brittany, Brière, Anjou, Sologne, Vendée, Limousin. Muscle tissue samples were obtained from 91 trapped or road-killed animals provided by trappers, taxidermists and naturalist associations (DPN authorisation n°98/717/AUT). Crude extracts from tissue, macerated in equal volume of distilled water were centrifuged at 10,000g for 15 minutes at 4°. I performed an electrophoresis of soluble proteins by starch gel electrophoresis (Sigma) using three buffer systems, Tris-citrate pH6, Tris-citrate pH8 and Tris-EDTA-borate pH8 (see Lodé 1998). Slices were stained for 24 enzymes encoded by 38 gene structure

loci following Pasteur et al. (1987), Murphy et al. (1990) and Rothe (1994) procedures. Loci successfully resolved were *Aat-1* and *Aat-2* (EC 2.6.1.1), *Aco-1* and *Aco-2* (EC 4.2.1.3), *Ada* (EC 3.5.4.4), *Ak* (EC 2.7.4.3), *Ck-1* and *Ck-2* (EC 2.7.3.2), *Ddh-1* and *Ddh-2* (EC 1.8.1.4), *Est-1* and *Est-2* (EC 3.1.1.1), *Fumh* (EC 4.2.1.2), *Gly2dh* (EC 1.1.1.29), *G6pdh* (EC 1.1.1.49), *Gpi* (EC 5.3.1.9), *Hk-1*, *Hk-2* and *Hk-3* (EC 2.7.1.1), *Idh-1* and *Idh-2* (EC 1.1.1.42), *Ldh-1* and *Ldh-2* (EC 1.1.1.27), *Mdh-1* and *Mdh-2* (EC 1.1.1.37), *Me-1* and *Me-2* (EC 1.1.1.40), *Mpi* (EC 5.3.1.8), *Pep-1* and *Pep-2* (EC 3.4.11.1), *Pgdh* (EC 1.1.1.44), *Pgm-2* (EC 2.7.5.1), *Pnp* (EC 2.4.2.1), *Sdh* (EC 1.1.1.14), *Sod* (EC 1.15.1.1), *Tpi* (EC 5.3.1.1), and two non specific proteins. Out of numerous allozymes examined, five of them could not be scored consistently and therefore were excluded. They were considered as unsuccessful ones when they showed a too diffuse zone of activity or when no activity was detected.

F-statistics were assessed using **F-STAT** (Goudet, J. 2000. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.1. updated from Goudet 1995), **GENETIX** (Belkhir, K., Borsa, P., Goudet, J., Chikhi, L. and Bonhomme F. 1996-98, Genetix version 3.3, Laboratoire Génome and Populations, CNRS UPR 9060, Montpellier France,) and **POPGEN32** software (Yeh, F., Yang, R.C., Boyle, B.J. Ye, Z.H. & Mao, J.X., 1997, Pop Gen 3.2. Mol Biol Biotech Centre, Univ Alberta). The effective number of alleles was estimated as in Kimura and Crow (1964) revised by Nei (1987). Observed H_O and expected $H_{E(n.b.)}$ non biased average heterozygosities (Nei, 1978) over loci were calculated and heterozygote deficiency (inbreeding) was based on the F_{IS} index as in Wright (1978) and Weir and Cockerham (1984). F_{IS} value was calculated using 1000 permutations of alleles within population for each locus (Genetix procedure). The relatedness within subpopulations (*Relat*), regarding either males (n = 54) or females (n = 37), was assessed using Queller and Goodnight's (1989) estimator as relatedness = 2 F_{ST} / (1+F_{IT}) (with q, see Weir and Cockerham 1984) and using jack-knifing procedure over loci R_J (Weir 1996).

RESULTS

Mating system In male polecat, the rutting period began in February as revealed by change in the size of testes. During oestrus, receptive females exhibited a strong congestion of the vulva associated with the follicular maturation. Most of copulations occurred from March to mid-April and parturitions, as revealed by recaptures of lactating females, happened from May to June.

The size of the activity area averaged 2.53km² (sd 1.76) in males (n = 8) while the range only reached 0.74km² (sd 0.25) in females (n = 10). However, movements were very contrasted among males. Two types of movements characterized the spatial pattern. Numerous repeated locations in restricted areas were followed by several long distance travels. But, while some males returned to their previous range, other males were located far from their former fixes and five of them left out of the area. Diel movements of males, averaging 152.9m (sd 102.6) were larger than those of females averaging 63.2m (sd 51.2) (Welch alternate *t* test = 2.39, df11 p = 0.036) but in males, some movements exceeded 6.1 km. Female polecats also displayed series of sinuous small tracks alternating with longer straight ones but distances were smaller than males and females tended to stay on the same area. Oestrous females reduced their nocturnal movement.

Most of male polecats moved across several female contiguous ranges but consortship success varied among males. The minimal consortship duration ranged from one to six days and averaged 2.85 (sd 1.57) (Fig. 1). Even considering mating season and reproductive adults, consortship behaviour remained uncommon and only represented 4.0% (sd 4.8%) of the survey length. Male polecats successively consorted with an average of 1.44

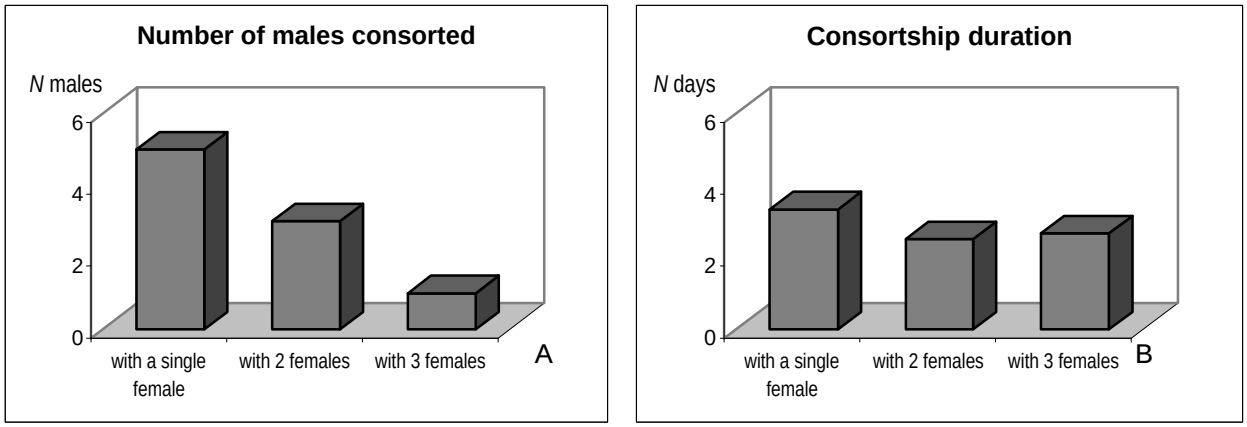

Fig.1. A. Number of males successfully consorted with females and B. Minimal consortship duration among males in the European polecat in western France.

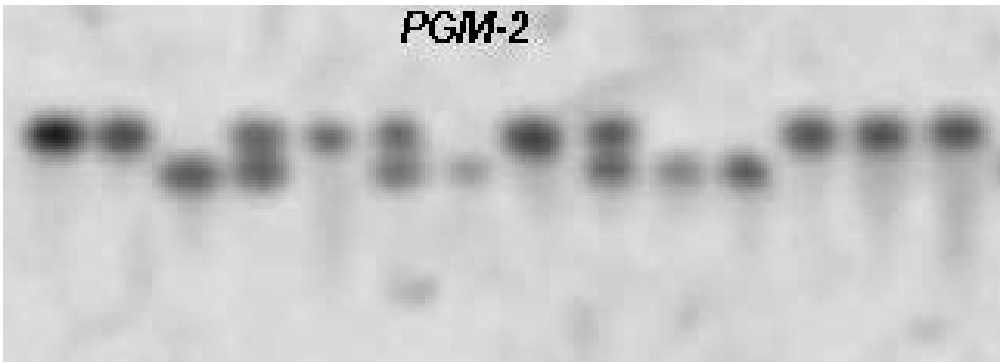

Fig. 2. Electrophoretic activity of a polymorphic locus (PGM-2) showing two band pattern for heterozygotes, in *Mustela putorius* populations from France.

females (sd 0.73), but 55.6% of males consorted with a single female while 33.3% were with 2 females and only one consorted with three females. Each female only consorted with a single male. Variations in consortship duration tended to be longest when male stayed with only one female but the test among males was not significant (Kruskal-Wallis = 0.94, p = 0.65).

Genetic variance Out of 38 loci, nine were found polymorphic (23.7%) at p = 0.05 (*Ada, Est-2, G6pdh, Mdh-1, Me-1, Pep-2, Pgm-2, Pnp and Sdh*). *Ada* was coded by one monomeric locus showing one band or two for heterozygotes. For Esterase, two zones of activity were found corresponding to two monomeric loci of which only *Est-2* was polymorphic. Only one band was discovered for the homozygotes in the dimeric locus of *G6pdh*. Heterozygote showed an intense band and two reduced outer bands. Tissue expressed two activity zones corresponding to two dimeric loci (*Mdh-1 and Mdh-2*), each one having a heavy band and a weaker band for homozygotes. Two malic enzyme isozymes have been observed with one band for homozygotes in *Me-1* and three weaker bands for heterozygotes. *Pep-2* was a dimeric locus and heterozygotes were revealed by one heavy band and two weaker ones while *Pep-1* most anodal was monomorphic. *Pgm*

Table 1. Allelic frequencies and sample sizes for 9 variable loci in *Mustela putorius* from western France, (a, b and c referred to electrophoretic mobility of alleles)

Locus	alleles	frequencies	N
ada	a	0.495	*91*
	b	0.506	
est-2	a	0.105	*76*
	b	0.895	
g6pgdh	a	0.883	*64*
	b	0.117	
mdh-1	a	0.724	*87*
	b	0.040	
	c	0.236	
me-1	a	0.714	*89*
	b	0.287	
np	a	0.560	*91*
	b	0.440	
pep-2	a	0.907	*70*
	b	0.093	
pgm-2	a	0.861	*86*
	b	0.139	
sdh	a	0.600	*85*
	b	0.400	

Table 2. Polymorphism, number of alleles, observed (Ho), expected heterozygosity (H_E) and F_{IS} index for 9 polymorphic loci in six polecat populations from western France

Population name	**Anjou**	**Vendée**	**Brière**	**Brittany**	**Limousin**	**Sologne**	**MEAN Values**
Polymorphism at 0.05	*21%*	*21%*	*18.4%*	*18%*	*16%*	*18%*	*23.7%*
Number of alleles	1.24	1.24	1.18	1.21	1.16	1.18	1.263
H_o	**0.065**	**0.053**	**0.058**	**0.030**	**0.046**	**0.047**	**0.051**
Sd	*0.159*	*0.114*	*0.136*	*0.065*	*0.115*	*0.131*	*0.0112*
$H_{E\,(n.b.)}$	0.077	0.072	0.068	0.059	0.078	0.076	0.082
Sd	*0.160*	*0.144*	*0.153*	*0.128*	*0.181*	*0.175*	0.163
F_{IS}	0.165	0.269	0.150	0.508	0.425	0.385	0.383
N individuals	*20*	*14*	*12*	*16*	*14*	*15*	*91*

was encoded by two loci but one activity zone for monomer *Pgm-2* was detected exhibiting one band for homozygotes (Fig. 2). *Pnp* coded by one trimeric locus showing a three banded pattern. The zymogramme of *Sdh* consisted of one band for one dimeric locus. The less frequent allelic frequency only reached 4% for *Mdh-1* (Table 1).

The observed heterozygosity averaging H_O = 0.051, ranged from H_O = 0.030 in Brittany to H_O = 0.065 in Anjou (Table 2). The observed heterozygosity showed a low level whereas non biased expected heterozygosity (mean $H_{E\ (nb)}$ =0.082) had always a higher value, ranging from $H_{E\ (nb)}$ = 0.059 to $H_{E\ (nb)}$ = 0.082. By the way, the F_{IS} index averaging 0.383 revealed a deficit of heterozygotes in every population. The F_{IS} index was 0.425 in Limousin and extended to 0.508 in Brittany. The heterozygote deficiency remained lower in Brière with 0.150 but reached 0.165 in Anjou.

The observed mean heterozygosity did not differ between males (H_O = 0.049, n = 54) and females (H_O = 0.053, n = 37). The estimate of the mean relatedness averaged *Relat* = 17% and R_J = 17.4% (sd 4.0) using jack-knifing procedure over loci. However, male polecats showed a lower level of relatedness reaching only 13.2% (R_J = 13.5% jack-knifing sd 4.7, n = 54). By contrast, relatedness was 21.2% in females (R_J = 21.2% jack-knifing sd 9.0, n = 37) revealing a great disparity between sexes since females were almost twice more related than males (Welch's approximate *t* test = 4.8, df 49 $p < 0.0001$).

DISCUSSION

Mating system. The mating system of European polecat is characterized by a strategy of successive polygyny and a single male can consort with one to three receptive females. Mustelids have often been portrayed as polygynous species but mating behaviour has rarely been reported from wild populations because such observations are difficult for most solitary and nocturnal species (Hillman and Carpenter, 1984; Sandell, 1986, 1989 Lodé, 1996). However, the pattern of space use showing numerous locations on very restricted areas alternating with long distance travels is often typically observed in mustelids and males generally occupy larger ranges than those of females (Sandell, 1989; Weber, 1989, Sasaki and Ono, 1994; Birks and Kitchener, 1999; Lodé 1993, 2000). During the breeding period, the extent of the activity area was directly related to the increase of movements. In stoats, mating season also influences spatial pattern (Sandell, 1983; Robitaille and Raymond, 1995) and male mustelids often range widely during the mating season (Gerell, 1970; Weber, 1989, Robitaille and Raymond, 1995; Garin et al., *in press*). From results, it is suggested that male polecats enlarged their movements searching for mate opportunities. Such behaviour provided an explanation on the apparent discrepancies in the home range size and of the long-distance travels sometimes exceeding several kilometers in numerous mustelids (Gerell, 1970; Skinisson, 1986; Weber, 1989; Samson and Raymond, 1998; Garin et al., *in press*). Polecats exhibited very solitary habits and the consortship duration remained very brief. Radiotracking data revealed that multiple consortship males could succeed because they resided in the vicinity of several oestrous females. The number of receptive females can be regarded restricting on the breeding of males. Thus it could be predicted that the stability of receptive female range affects decisively the consortship success of males. The main strategy for male polecats consists of short-term mating excursions in adjacent female ranges. This pattern has already been described in male stoats (Sandell, 1983) and, despite being rarely reported in literature for free ranging carnivores, it could be suspected to be the most frequent strategy adopted by male polygynous carnivores. Therefore male polecats often moved within their range and alternatively can launch upon long distance travels outside their range searching for receptive females. Unfortunately how consortship behaviour is related to breeding success remains unknown. Nevertheless, this alternative strategy resulted in few consortships and is expected to be poorly efficient. Because they leave their home range, these males are presumed to be poor competitors for mate. It remained to be seen whether such males avoided dominant males or whether females evicted them. In any cases, such subordinate adults may only gain some advantage by dispersing. Competitive interactions could be costly in carnivores and may favour the size dimorphism of polecats.

Genetic variance. Allozymic variation of polymorphic loci were consistent with those reported for carnivores (O'Brien, 1980; Simonsen, 1982; Hartl et al., 1988; Evans et al., 1989; Mitton and Raphael, 1990; Kennedy et al, 1991; Randi et al., 1993). Despite a high level of allozymic polymorphism (24%), polecat populations exhibited a clear heterozygote deficiency. Although Simonsen (1982) found no allozymic variation in seven species of carnivores from Denmark, heterozygosity level in polecat was within the range reported in most mustelids (Hartl et al., 1988; Serfass et al., 1998; Wilson et al., 2000). The heterozygote deficit occurred in every population but in polecat, the heterozygosity levels were found to be associated with habitat diversity (Lodé 1998, 2001). The strong inbreeding as revealed by the F_{IS} index may result from mating strategy. The overall relatedness averaging 17% in polecat was lower than that observed in carnivores living in social groups such as wolves (*Relat* >25%, Lehman et al., 1992). From relatedness analysis, our results suggest that males were the dispersing sex in polecats. Breeding dispersal was sex-biased with males being almost twice less related than females (13% versus 21%). The

general pattern of male-biased dispersal while females are more philopatric is often admitted in numerous mammals and regarded as favouring inbreeding avoidance (Greenwood, 1980; Waser and Jones, 1983; Johnson and Gaines, 1990; Keane et al., 1996). Nonetheless, from this general theme, breeding dispersal patterns showed wide variations and revealed a more complex situation. In polecat, mating short-term excursions were frequent in adjacent female home ranges. Resident males may visit several females in contiguous home ranges but returned within a few days. Because of female philopatry, such mating may increase inbreeding probability. Dispersal mechanisms are also insufficient to avoid incestuous copulation in Black bear (Rogers, 1987). Natal dispersal in which juveniles search to settle far from their natal home-range is often distinguished from breeding dispersal in which adults search for increasing their mate opportunities (Greenwood, 1980). Because polecats are mature in their first winter, this difference is not obvious. Inbreeding avoidance chiefly depends on long-distance dispersal, which has been expected to be the main pattern in polygynous carnivores. Conversely, short-breeding excursion was found to be the main breeding pattern in polecat whereas long-distance travel occurs less frequently. Patterns of dispersal in breeding mustelids are mainly expected to proceed according to the stepping-stone model in which sub-population exchanges are favoured in contiguous zones (Gadgil, 1971). Moreover, it could be assumed that subordinate males leaving their range for better opportunities to mate are poor competitors and have a low consortship success. Despite the one migrant per generation rule (Wright, 1943; Mills and Allendorf, 1996), this breeding dispersal appeared poorly efficient to retain genetic diversity. The respective role of competitive interactions among males and of female choice in the adoption of these male alternative strategies should be however detailed.

Because of their large sexual dimorphism, their mating system and their intolerance, polecats could be considered as typical polygynous and solitary carnivores. Both the female philopatry and the fact that resident males succeed in multiple consortships may result in an increase of heterozygote deficit. Thus the mating system of such solitary mustelids may be poorly efficient to prevent inbreeding.

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REFERENCES

Birks, J. D. S., and Kitchener, A. C. (1999) The distribution and status of the polecat *Mustela putorius* in Britain in the 1990s. The Vincent Wildlife Trust, London.

Evans, P. G. H., MacDonald, D. W., and Cheeseman, C. L. (1989) Social structure of the European Badgers *Meles meles* : genetic evidence. J. Zool. Lond. **218**, 587-595.

Forbes, S. H., and Boyd, D. K. (1996) Genetic variation of naturally colonizing wolves in the central rocky mountains. Conserv. Biol. **10**, 1082-1090.

Frame, L. H., Malcolm, J. R., Frame, G. W., and van Lawick, H. (1979) Social organization of African wild dogs (*Lycaon pictus*) on the Srengeti Plains, Tanzania, 1967-1978. Z. Tierpsychol. **50**, 225-249.

Gadgil, M. (1971) Dispersal: population consequences and evolution. Ecology, **52**, 253-260.

Garin, I., Zuberogoitia, I., Zabala, J., Aihartza, J., Clevenger, A. P. & Rallo, A. (2001) Home range of European mink (Mustela lutreola) in Southwestern Europe. Acta theriol *in press*

Gehrt, S. D., and Fritzell, E. K. (1999) Behavioural aspects of the raccoon mating system: determinants of consortship success. Anim. Behav. **57,** 593-601.

Gerell, R. (1970) Home range and movements of the mink *Mustela vison* in southern Sweden. Oikos **21**, 160-173.

Gompper, M. E., Gittleman, J. L., and Wayne, R. K. (1997) Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. Anim. Behav. **53**, 781-797.

Gotelli,D., Sillero-Zubiri, C., Applebaum, G. D., Girman, D., Roy, M., Garcia-Moreno, J., Ostrander, E., and Wayne, R. K. (1994) Molecular genetics of the most endangered canid, the Ethiopian wolf *Canis simensis.* Mol. Ecol. **3**, 301-312.

Greenwood, P. J. (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. **28**, 140-1162.

Hartl, G. B., Willing, R., Grillitsch, M., and Klansek, E. (1988) Biochemical variation in Mustelidae: Are carnivores genetically less variable than other mammals. Zool. Anz. **221**, 81-90.

Herrera, E. A., and MacDonald, D. W. (1993) Aggression, dominance, and mating success among capybara males (*hydrochaeris hydrochaeris*). Behav. Ecol. **4**, 114-119.

Hillman, C. N., and Carpenter, J. W. (1984) Breeding biology and behaviour of captive Black-footed ferrets *Mustela nigripes*. Inter Zool Yearbook **23**, 186-191.

Johnson, M. L., and Gaines, M. (1990) Evolution of dispersal: theoretical models and empirical tests using birds. Ann. Rev. Ecol. Syst. **21**, 449-480.

Keane, B., Creel, S. C., and Waser P. M. (1996) No evidence of inbreeding avoidance or inbreeding depression in a social carnivore. Behav. Evol. **7**, 480-489.

Kennedy, P. K., Kennedy, M. L., Clarkson, P. L., and Liepins, I.S. (1991) Genetic variability in natural populations of the gray wolf, *Canis lupus*. Can. J. Zool. **69**, 1183-1188.

Kimura, M., and Crow, J. F. (1964) The number of alleles that can be maintained in a finite population. Genetics **49**, 725-738.

Lehman, N., Clarkson, P., Mech, L. D., Meier, T. J., and Wayne, R. K. (1992) A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. Behav. Ecol. Sociobiol. **30,** 83-94.

Lodé, T. (1990) Reconnaissance du congénère et comportement sexuel chez le Putois. Bull. Soc. Sc. Nat. Ouest France **12,** 105-110.

Lodé, T. (1993) Diet composition and habitat use of sympatric

polecat and American mink in western France. Acta Ther. 38,161-166.

Lodé, T. (1994) Environmental factors influencing habitat exploitation by the polecat *Mustela putorius* in western France. J. Zool., London **234**, 75-88.

Lodé, T. (1995) Activity pattern of polecats *Mustela putorius* L. in relation to food habits and prey activity. Ethology **100,** 295-308.

Lodé, T. (1996) Conspecific tolerance and sexual segregation in European polecat. Acta Theriol. **41**, 171-176.

Lodé, T. (1998) Genetic heterozygosity in polecat *Mustela putorius* populations from western France. Hereditas **129,** 259-261

Lodé, T. (2000) Functional response and area-restricted search of a predator : seasonal exploitation of anurans by European polecat *Mustela putorius.* Autral Ecol. **25**, 223-231.

Lodé, T. (2001) Genetic divergence without spatial isolation in polecat *Mustela putorius* populations. J. Evol. Biol. **14**, 228-236.

Mills, L. S., and Allendorf, F. W. (1996) The One-Migrant-per-Generation rule in conservation and management. Conserv. Biol. **10**, 1509-1518.

Mitton, J. B., and Raphael, M. G. (1990). Genetic variation in the marten, *Martes americana.* J. Mammal. **71**, 195-197.

Mohr, C. O. (1947) Table of equivalent populations of North American small mammals. Am. Midl. Nat. **37**, 223-249.

Murphy, R. W., Sites, J. W., Buth, D. G., and Haufler, C. H. (1990) Proteins. I : Isozyme electrophoresis. In: Molecular systematics (eds.: Hillis and Moritz), pp. 45-126. Sinauer Press, Sunderland.

Nei, M. (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583-590.

Nei, M. (1987) Molecular Evolutionary Genetics. Columbia University Press, New York.

O'Brien, S. J. 1980. The extent and character of biochemical genetic variation in the domestic cat. J. Hered. **71**, 2-8.

Packer, C., and Pusey, A.E. (1993) Dispersal, kinship, and inbreeding in African Lions. In: the natural history inbreeding and outbreeding (eds: N.W. Thornhill), pp.375-391. Univ. of Chicago Press, Chicago.

Pasteur N, Pasteur G, Bonhomme F, Catalan J, and Britton-Davidian J. (1987) Manuel technique de génétique par électrophorèse des protéines. Paris: Lavoisier.

Poole, T. B. (1974) Detailed analysis of fighting in polecats (Mustelidae) using cine film. J. Zool. Lond. **173**, 396-393.

Queller, D. C., and Goodnight, K. F. (1989) Estimating relatedness using genetic markers. Evolution **43**, 258-275.

Ralls, K. (1977) Sexual dimorphism in mammals : avian models and underanswered questions. Am. Nat. **111**, 917-938.

Randi, E., Lucchini, V., and Francisci, F. (1993) Allozyme variability in the Italian wolf (*Canis lupus)* population. Heredity **71**, 516-522.

Robitaille, J. F., and Raymond (1995) Spacing patterns of ermine, *Mustela erminea* L., in a Quebec agrosystem. Canad. J. Zool. **73**, 1827-1834.

Rogers, L. L. (1987) Factors influencing dispersal in the Black bear. In: Mammalian dispersal pattern (eds.: B. D. Chepko and Z. T. Halpin) pp. 75-84. Unive. Of Chicago Press, Chicago.

Rood, J. P. (1989) Male association in a solitary mangoose. Anim. Behav. **38**, 725-727.

Rothe, G. M. (1994) Electrophoresis of enzymes, laboratory methods. Springer-Verlag, London.

Samson, C., and Raymond, M. (1998) Movements and habitat preference of radio tracked stoats, *Mustela erminea* during summer in southern Québec. Mammalia **62,** 165-174.

Sandell, M. (1983) Alternative mating strategies of male stoats. Acta Zool. Fennica **174**: 173-174.

Sandell, M. (1986) Movement patterns of male stoat *Mustela erminea* during the mating season: differences in relation to social status. Oikos **47**, 63-70.

Sandell, M. (1989) The mating tactics and spacing patterns of solitary carnivores. In: Carnivore behavior, ecology, and evolution. (ed J. L. Gittleman) pp. 164-182. Cornell University Press, New York.

Sasaki, H., and Ono, Y. (1994) Habitat use and selection of the siberian weasel *Mustela siberica coreana* during the non mating season. J. Mamm. Soc. Japan **19**, 21-32.

Serfass, T. L., Brooks, R. P., Novak, J. M., Johns, P. E., and Rhodes, O. E. (1998) Genetic variation among populations of river otters in North America: considerations for reintroduction projects. J. Mammal. **79**, 736-746.

Simonsen, V. (1982). Electrophoretic variation in large mammals. II. The red fox, *Vulpes vulpes*, the stoat, *Mustela erminea*, the weasel, *Mustela nivalis*, the polecat, *Mustela putorius*, the pine marten, *Martes martes*, the beech marten, *Martes foina*, and the badger, *Meles meles*. Hereditas **96**, 299-305.

Smale, L., Frank, L., and Holekamp, K. E. (1993) Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relationships with adult females and immigrant males. Anim. Behav. **46**, 467-477.

Skirnisson, K. (1986) Untersuchungen zum Raum-Zeit System freilebender Steinmarder (*Martes foina* Erxleben, 1777). Beitr. Wildbiol. **6**, 1-200.

Thirgood, S. J. (1990) Alternative mating strategies and reproductive success in fallow deer. Behaviour **116**, 1-9.

Vuuren, van B. J., and Robinson, T. J. (1997) Genetic population structure in the yellow mongoose, *Cynictis penicillata*. Mol. Ecol. **6**, 1147-1153.

Waser, P. M., and Jones, W. T. (1983) Natal philopatry among solitary mammals. Q. Rev. Biol. **58**, 355-390.

Weber, D. (1989) Foraging in polecats *Mustela putorius* L. of Switzerland: the case of a specialist anuran predator. Z. Säugetierk. **54,** 377-392.

Weir, B. S. (1996) Genetic data analysis II. Sinauer Publ., Sunderland, MA.

Weir, B. S., and Cockerham, C. C. (1984) Estimating F-statistics for the analysis of population structure. Evolution **38**, 1358-1370.

White, G. C., and Garrott, R. A. (1990) Analysis of wildlife radio-tracking data. Academic Press, New York.

Wilson, G. M., Van Den Bussche, A., Kenedy P. K., Gunn, A. and Poole, K. 2000. Genetic variability of wolverines (*Gulo gulo*) from the northwest territories, Canada: conservation implications. J. Mammal. **81**, 186-196.

Woodroffe, R., Mac Donald, D. W., and Da Silva, J. (1995) Dispersal and philopatry in the European badger. J. Zool. Lond. **237**, 227-239.

Wright, S. (1943) Isolation by distance. Genetics **28**, 114-128.

Wright, S. (1978) Evolution and the genetics of populations. IV. Variability within and among natural populations. University Press, Chicago.

Zabel, C. J., and Taggart, S. J. (1989) Shift in red fox, *Vulpes vulpes,* mating system associated with El Ni o in the Bering Sea. Anim. Behav. **38**, 830-838.