

MULTIPLE PATERNITY AND REPRODUCTIVE TACTICS OF FREE-RANGING AMERICAN MINKS, *MUSTELA VISON*

NOBUYUKI YAMAGUCHI, RONALD J. SARNO, WARREN E. JOHNSON, STEPHEN J. O'BRIEN, AND DAVID W. MACDONALD*

Wildlife Conservation Research Unit, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom (NY, DWM)
Laboratory of Genomic Diversity, National Cancer Institute, Frederick, MD 21702-1201, USA (RJS, WEJ, SJO)

Present address of RJS: Department of Environmental Science and Interdisciplinary Studies Program,
University of South Florida, Tampa, FL 33620, USA

Demography and spatial patterns of free-ranging American mink were documented by continuous year-round trapping and radiotracking along 24 km of the River Thames in England, United Kingdom. An estimated average of 7.19 ± 0.58 SE minks per month were present between May 1995 and August 1997. Kit and juvenile paternity was assessed using 7 microsatellite markers and we observed evidence that multiple paternity occurred in this population. Although males maintained territories during most of the year, they sired litters in areas beyond their territory boundaries. We suggest that a male's inability to monopolize paternity, along with a female's ability to continue ovulation after successful matings (i.e., superfetation) explains why males abandon territoriality during the breeding season. We suggest that the main function of a brief delayed implantation of this species may be to enable female mink to retain superfetation, which facilitates the fertilization of ova from different ovulations by different males. This mink model, consisting of disarticulating residency from fatherhood and the possibility of superfetation, may occur more widely among related species and requires a re-evaluation of mustelid sociobiology.

Key words: American mink, delayed implantation, intrasexual territoriality, lowland England, *Mustela vison*, spatial organization, superfetation, superfecundation

The spacing pattern in carnivore populations commonly results from individual tactics that maximize survival and reproductive success (Macdonald 1983; Sandell 1989). Generally, female spacing patterns are determined by food and possibly shelter, whereas male spacing is governed by the dispersion of females. In some species, however, including American mink (*Mustela vison*), males' spatial patterns change seasonally depending on the availability of different decisive resources (Bailey et al. 1986; Erlinge and Sandell 1986; Robitaille and Raymond 1995; Schröpfer et al. 1997; Taylor and Abrey 1982). Free-ranging minks of both sexes defend intrasexual territories during the nonbreeding season, when a male's territory overlaps with those of a few females (Dunstone 1993; Gerell 1970; Ireland 1988). This spatial arrangement is typical of most Mustelidae (Johnson et al. 2001; Powell 1979, 1994). While female minks maintain their territories throughout the breeding season, many males abandon their prebreeding territories to roam over larger areas (Birks 1981; Dunstone 1993; Ireland 1988). At the end of the breeding

season, the roaming males settle down and some hold territories until the following breeding season (Birks 1981; Dunstone 1993; Ireland 1988). It has been widely concluded that roaming males are searching for receptive females (Erlinge and Sandell 1986; Sandell 1986; Schröpfer et al. 1997), but more concrete evidence (e.g., molecular evidence of the reproductive consequences) to support this hypothesis is lacking.

In general, males are thought to maximize their mating success by guarding females from rivals and by seeking extra-pair copulations (Brotherton and Manser 1997; Henzi et al. 1998; Komdeur et al. 1999). It is also assumed that resident males achieve almost all matings in carnivore populations (Sandell 1989). Therefore, considering the intrasexual territoriality of mink, an explanation may be necessary for males' abandoning their territories during the breeding season. Males might have mated with the local females before vacating, thereby retaining the reproductive benefit of maintaining a territory. Roaming males may also settle in a territory overlapping females they have inseminated, as suggested for another mustelid, the European pine marten (*Martes martes*—Schröpfer et al. 1997). This explanation of male–female overlap argues that the male protects his investment from harassment, including infanticide, by unrelated males (Andelman 1986; Armitage 1986; Packer et al. 1988; Wrangham and Rubenstein 1986). In summary, these two hypotheses, which may not be

* Correspondent: david.macdonald@zoo.ox.ac.uk

mutually exclusive, predict that kits will be fathered by males that overlap territories with their mothers either before or after the breeding season.

American minks breed once yearly and, in Britain, mating occurs between late February and early April, a period during which every female is believed to remain receptive (Birks 1981; Dunstone 1993; Ireland 1988; Shackelford 1952; Venge 1973). A short delay in implantation prolongs the 34- to 38-days active gestation between implantation and parturition (Tauson et al. 1988). Then, 5–8 kits are born between late April and mid-May (Dunstone 1993). In ranched minks, ova from a single ovulation can be fertilized by ≥ 1 male when other males mate within 1–3 days of the initial mating, a phenomenon known as superfecundation (Shackelford 1952; Venge 1973). Furthermore, female American minks continue to ovulate after the initial fertilization if ≥ 6 days elapse between matings, and kits can be sired by ≥ 2 males that fertilize the ova of different ovulations: a phenomenon called superfetation (Dunstone 1993; Mead 1994; Shackelford 1952). The earlier the fertilization occurs, the longer is the delay until implantation, decreasing the survival of fertilized eggs (Shackelford 1952; Venge 1973). Hence, the later a male mates, the greater the proportion of the litter he is likely to sire (Shackelford 1952; Venge 1973). Confirmed reports of natural superfetation are extremely rare and, apart from the American mink, has been described only in the casiragua (*Proechimys semispinosus*—Weir 1974), the North African gundi (*Ctenodactylus gundi*—Gouat 1985), and the brown hare (*Lepus europaeus*—Caillol et al. 1991). However, superfetation in these 3 species is characterized by a 2nd estrus just before parturition that resulted from the first set of ova. Therefore, although the 2nd ovulation occurs before parturition, each set of ova develop separately in essentially 2 different pregnancies, in a fundamentally different process from that of the American mink. In contrast with the depth of our understanding of ranched mink, little is known of their reproductive biology in the wild, including whether or not multiple paternity occurs in free-ranging American mink populations.

Among the 15 mustelids known to exhibit delayed implantation, only the American mink experiences a very short delay. In contrast with the 6–11-month delay of the other 14 species, that of mink is variable up to only 35 days and mink ova fertilized at the end of the mating season may implant without any delay (Dunstone 1993; Mead 1981; Sandell 1990). Conventionally, 2 nonexclusive hypotheses for the function of delayed implantation both assume an optimal birth season for offspring survival. It may be advantageous to shift the birth season forward from the mating season or to shift the mating season backward from the birth season either to adjust to climatic conditions (Ben-David 1998; Mead 1993) or to take advantage of periods of maximum mate choice (Sandell 1989). Both hypotheses view delayed implantation as a means of adjusting the period between mating and birth. Neither hypothesis, however, satisfactorily explains a delay as brief as that of American mink. In the mink's case, if multiple paternity facilitated by superfetation occurs in the wild, then most kits would originate from ova fertilized toward the end of the mating season. When females mate twice within an interval between 7

and 28 days, less than 10% of kits are sired by the first male (Mead 1994; Shackelford 1952). Thus, in practice, the delay in implantation of mink ova may often be much shorter even than the 35-day maximum, which is difficult to interpret as a means of such an adjustment.

In this paper, we examine 3 questions: whether multiple paternity occurs in a free-ranging mink population, whether male minks hold territories during the nonbreeding season because it benefits males' reproductive success during the following breeding season, and whether males do so because it benefits male reproductive success by providing protection to offspring from the previous breeding season. From an evolutionary perspective, we evaluate why males abandon their territories during the breeding season although these territories overlap those of a few females, and the functional advantage of the short delayed implantation to female mink.

MATERIALS AND METHODS

Sexing, aging, and classification of mink.—The study site consisted of about 24 km along the River Thames (51°40'N, 1°25'W), west of Oxford City, Oxfordshire, England, United Kingdom. We collected data between May 1995 and August 1997 to investigate demography and individual spacing patterns of free-ranging American mink by continuous year-round trapping (on average, a trap was set every 200 m along the watercourses) and radiotracking. All animals were identified using the ventral white spot patterns (Birks 1981; Dunstone 1993; Ireland 1988), and sex and age classes (adult, juvenile, and kit) were recorded. Mink were classified as kits if observed or trapped with their mothers before dispersal (occurring around 13-weeks of age in early August), after as juveniles until the onset of the first breeding season (at approximately 8-months of age in January), and after as adults. The age class of a newly caught individual was assessed in males by toothwear and baculum length, and for females by toothwear and the presence of white mating hairs on the neck (Dunstone 1993; Ireland 1988). Following Hatler (1976) and Ireland (1988), females present in the area for ≥ 3 consecutive months were classified as residents. Because of their suggested seasonal changes in spacing patterns (Birks 1981; Dunstone 1993; Ireland 1988), males were classified as residents only if they were in the study area for ≥ 3 consecutive months in the nonbreeding season (May–December). Others were classified as transients. We consider that the proportion of animals trapped was $\geq 80\%$ of those present (Yamaguchi and Macdonald 2003).

Sample collection.—Mink were captured with commercial, single-entry aluminum mink and rat cage traps, approximately 14 × 14 × 76 cm (A. Fenn and Co., Redditch, Worcestershire, United Kingdom). Trapped mink were transferred to an anesthesia box with clear acrylic (Perspex) sides (approximately 15 × 15 × 48 cm). Cotton wool soaked with methoxyfluorane (Metofane, C-Vet Ltd., Bury St. Edmunds, Suffolk, United Kingdom) or isoflurane (IsoFlo, Mallinckrodt Veterinary Ltd., Uxbridge, Middlesex, United Kingdom) was put into the box to induce anesthesia followed by an intramuscular injection of 0.2–0.3 ml medetomidine (Domitor, Orion Corporation, Farmos, Turku, Finland) and ketamine (Vetalar, Parke, Davis, and Company, Pontypool, Gwent, United Kingdom; 3:2 in volume, 0.2 ml per kg). Under anesthesia, a blood sample of ≤ 3 ml ($\leq 10\%$ of the total blood volume) was taken from the jugular vein using a 5-ml disposable plastic syringe with a 0.6 × 25 mm disposable needle (Terumo Europe N.V., Leuven, Belgium), transferred into a glass tube coated with ethylene diaminetetraacetic acid (EDTA; Becton Dickinson Vacutainer Systems Europe, B.P.No.37, Meylan Cedex, France), and cooled with ice in the

field. The blood was then centrifuged at $3,000 \times g$ for 5 min to separate plasma from the blood cells, which were stored at -70°C . A skin sample from the ear was also collected using 3-mm-diameter biopsy punch (Stiefel Laboratories (UK) Ltd., Wooburn Green, Buckinghamshire, United Kingdom), then stored in BLB (250 mM EDTA, 5% SDS [sodium dodecyl sulphate], 50 mM Tris.Cl (pH 8.0); 2-amino-2-(hydroxymethyl)propane-1,3-diol, pH adjusted appropriately with HCl, autoclaved), and was stored at -70°C .

Investigation of the spatial patterns.—Range overlap between mink was investigated by radiotracking and retrapping. Locations of the radiotracked animals were determined every 15 min using waterproof radiocollars (Biotrack Ltd., Wareham, Dorset, United Kingdom), M57 receivers, and 3-element Yagi antennas (Mariner Radar Ltd., Lowestoft, Suffolk, United Kingdom). Also, if trapping revealed the most downstream capture point of animal A was downstream to the most upstream capture point of animal B, it was assumed that these 2 animals' home ranges at least partly overlapped. Birks and Linn (1982) reported that mink radiotracked at least twice a day revealed more than 80% of their total home ranges in ≤ 5 days and the entire home ranges in ≤ 10 days. We included only individuals that were radiotracked for either ≥ 10 days or that were followed, on average, for ≥ 20 hours a day for ≥ 5 days during the tracking periods (criteria met by 13 animals out of a total of 24 to which radiotransmitters were fitted). Comparable with other studies of mink (e.g., Birks and Linn 1982; Bonesi 1996; Gerell 1970; Ireland 1988) and otter (*Lutra lutra*—e.g., Durbin 1998) in semiaquatic habitat, we analyzed mink ranges on the assumption that they were linear along the water course. In this study, all radiolocations were allocated to 200- \times 50-m sections on both sides of the river (116 sections in total) covering all local water courses. The range size of each animal was calculated as the number of sections between the most-upstream and the most-downstream sections containing either radiolocation or capture point.

Mann-Whitney *U*-tests, corrected for ties, were used to assess differences between 2 categories, and Kruskal-Wallis tests when there were ≥ 3 categories, using StatView 4.01 software (Abacus Concepts, Inc., Berkeley, California). Binominal tests were used to assess whether kits are likely to be fathered by males that cohabit with their mothers either before or after the breeding season. Seasonal comparisons were made between breeding season (January–April) and nonbreeding season (May–December), and among early breeding season (January and February), late breeding season (March and April), kit-rearing season (May, June, and July), kit-dispersal season (August and September), and winter season (October, November, and December).

Paternity assessment.—Kits stay with their mothers until July or August (Dunstone 1993). Therefore, when kits were captured together with an adult female in the same trapping site at the same time or when juveniles were captured within a female's home range until late August, they were classified as her putative offspring. Genotypes of putative mothers and kits were compared to ensure that the molecular data were consistent with these assumptions. All resident males in the study area were tested for paternity of every kit and juvenile recorded in the study area during the nonbreeding season when the males were resident, and every kit and juvenile recorded in the following summer. All transient males recorded during the breeding season were tested for paternity of every kit and juvenile recorded in the study area in the following summer.

The genetic relationships between kits and juveniles and candidate fathers were investigated using 7 microsatellite markers. Total genomic DNA from either blood or the ear punches was extracted using standard phenol-chloroform methods (Sambrook et al. 1989). Products of 7 microsatellite loci were obtained by polymerase chain reaction (PCR)

TABLE 1.—Characteristics of 7 microsatellite loci used to analyze paternity in mink.

Locus	Number of alleles	Size range (base pairs)	Expected heterozygosity
Mvi111	9	90–114	0.861
Mvi114	9	71–89	0.707
Mvi219	4	165–175	0.470
Mvi232	6	145–161	0.657
Mvi24	4	132–140	0.247
Mvi54	8	91–129	0.706
Mvi87	8	74–88	0.771

amplification as described by O'Connell et al. (1996; Table 1). PCR products were electrophoresed on a 6% polyacrylamide gel using an ABI 373A automated DNA sequencer (Applied Biosystems Inc., Foster City, California), and data were collected and analyzed using the software programs GeneScan (version 1.2.2-1) and Genotyper (version 1.1). Microsatellite allele sizes were estimated by comparison with a GS350 TAMRA (Applied Biosystems Inc.) internal size standard. Putative parents were assessed using the program CERVUS 1.0 (Marshall et al. 1998). Only males for which there were no incongruencies in the inheritance of allele sizes in the kit, given the identified dam, were considered. Males were identified as the probable sire based on simulations (10,000 cycles); simulations assumed that about 80% of the candidate males were sampled, that 66% of the loci were typed, and that the rate of genotyping error was 1%. When more than 1 male was a possible sire with no mismatches, the paternity of the kit was classified as unresolved. If all males were excluded, the sire of the kit was classified as unsampled.

RESULTS

Demography of the population.—Twenty-seven males and 24 females were trapped in the study area a total of 184 times (4,336 trap nights) between May 1995 and August 1997, including 10 resident adult males, 13 resident adult females, 11 transient adult males, and 3 transient adult females. The population was unexploited by humans and an average of 7.19 ± 0.58 SE minks per month were present in the area, with 3.61 ± 0.35 males and 3.58 ± 0.34 females. On average, 1.64 ± 0.33 new minks were captured in the study area each month (0.93 ± 0.24 males and 0.71 ± 0.21 females), and 1.61 ± 0.32 individuals disappeared (emigration and death) from the study area each month (0.86 ± 0.19 males and 0.75 ± 0.21 females; Figs. 1a and 1b). The number of newly recorded adult males peaked in the early breeding season, January–February (Kruskal-Wallis test, $df = 4$, $H = 9.69$, $P = 0.046$), while there were no seasonal differences in adult females (Kruskal-Wallis test, $df = 4$, $H = 4.82$, $P = 0.31$). The disappearance of adult males also peaked in the early breeding season (Kruskal-Wallis test, $df = 4$, $H = 13.84$, $P = 0.008$) but did not vary by season for adult females (Kruskal-Wallis test, $df = 4$, $H = 6.95$, $P = 0.14$). All transient adult males and at least 8 of 10 resident adult males were not originally from the study area, and no resident adult male remained in his area of residence after the end of the early breeding season of the following year. All 3 male kits (and 5 out of 10 female kits) born in the study area disappeared before their first breeding season.

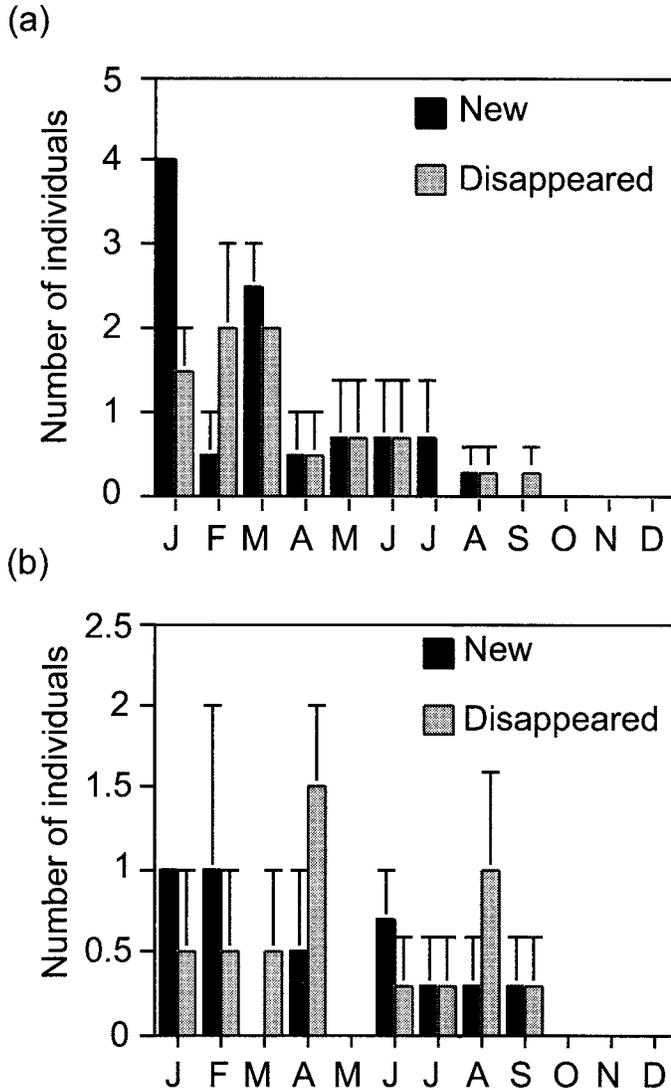


FIG. 1.—Changes in number of adults newly recorded in or that disappeared from the study area between May 1995 and August 1997 for a) males and b) females. Columns and bars represent means and SDs of changes during each month.

Range overlaps between resident adult males and resident females.—Minks were not distributed evenly throughout the study area, and most resident adults (21 out of 23) were found in 2 areas that were separated by an area used only occasionally by transient adults and juveniles (Fig. 2). The mean home range size of radiotracked resident adult males encompassed 6.80 ± 0.90 ($n = 3$) km of river. This was significantly longer than the 2.61 ± 0.59 ($n = 7$) used by radiotracked resident adult females (Mann–Whitney U -test, $n = 3$ and 7 , $U = 0$, $P = 0.016$). On average, a radiotracked resident adult male ($n = 3$) overlapped the home ranges of 3.3 ± 0.67 resident adult females during his residency. If resident juvenile females that would be capable of mating during the following breeding season were included, on average, a radiotracked resident adult male ($n = 3$) overlapped the home ranges of 3.7 ± 0.88 resident females.

Paternity.—For the 6 litters, each presumed to have been from 1 dam, the results were consistent with the occurrence of

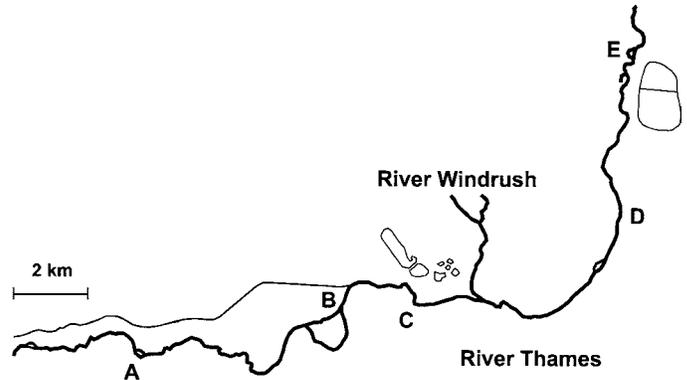


FIG. 2.—Distribution of resident adult mink in the study area in Upper Thames, England, United Kingdom. Resident males M5, M6, M12, M17, and M18 and resident females F2, F3, F5, F8, and F9 were recorded between Rushey Lock (A) and Shifford Lock (B). Resident males M3, M11, M16, and M19 and resident females F1, F4, F7, F10, F12, F13, and F14 were recorded between Thames Side Farm (C) and Bablock Hythe (D). Resident male M15 and resident female F11 were recorded around the downstream end of the study area (E).

multiple paternity (Table 2). For example, in 1996, litters of F3 and F4 were both sired by M8 and M9 and the litter of F10 was sired by M11 and ≥ 1 unsampled male indicating at least 3 out of 5 recorded litters of ≥ 2 kits were sired by ≥ 2 males. Also, a male's progeny were spatially widely dispersed: males M1 (mothers of his offspring: females F1 and F3), M8 (F3 and F4), and M9 (F3 and F4) had sired parts of litters that were widely separate (Fig. 2; Table 2). The most downstream point of F1's territory was about 12.5 km from the most upstream point of F3's territory, and the distance between those of F3 and F4 was about 10 km.

In addition, no recorded kits or juveniles were sired by a male that had been resident, prior to the mating season, in the territories occupied by their mothers ($n = 4$ male–female combinations; Table 2; Fig. 3). Although the small sample size does not enable us to reject definitively the null hypothesis that kits will be fathered by males whose territories overlapped with those of their mothers before the breeding season (binomial test, $n = 4$, $P = 0.06$), the results are notably inconsistent with this hypothesis. Furthermore, only in 1 case (out of 15 male–female combinations where a male might have set up his territory around that of the female might have produced his offspring; Table 2; Fig. 3) did a male subsequently take up residence in a territory overlapping a female carrying his young. The results statistically rejected the null hypothesis (binomial test, $n = 15$, $P = 0.0005$) that kits will be fathered by males that cohabit with their mothers after the breeding season.

DISCUSSION

Multiple paternity and male spacing patterns.—The results suggest that a territory of 1 resident male overlaps ≥ 3 territories of resident females, with which he potentially mates. Considering the probability that males had good chances to mate with resident females before they vacate their territories, why do they not continue to maintain their territoriality or at least remain nearby to repel other suitors (Sherman 1989)? One possibility is

TABLE 2.—Litters recorded in the study area and their mothers and fathers. Unresolved indicates that the sire could not be determined, and unsampled indicates that the sire was likely a male from which a sample was not obtained. Spatial overlap indicates that the male was recorded within the mother's territory before, during, or after the breeding season (see Figs. 2 and 3).

Year	Focal litter	Number of kits	Dam	Assigned sires (number of kits sired)	Spatial overlap
1995	Males tested: M1, M2, M3, M4, M5, and M6				
	1	4	F1	M1 (1) Unresolved (3)	During
	2	3	F3	M1 (2) Unresolved (1)	During
	3	1	F6	Unresolved	
1996	Males tested: M3, M5, M6, M7, M8, M9, M10, M11, M12, M13, M14, and M15				
	4	3	F3	M8 (1) M9 (1)	During During
	5	2	F4	M8 (1) M9 (1)	During During
	6	6	F10	M11 (2) Unsampled (3) Unresolved (1)	During and after

that the males and the females living in close vicinity may be related, and to avoid potential inbreeding, it may be beneficial for the males to leave the area to mate with unrelated females. Most male minks, however, keep moving their resident areas every year while females tend to stay in one area for longer periods (Hatler 1976; Ireland 1988; Fig. 3). In addition to this, juvenile males appeared to disperse further from their natal areas than did juvenile females. Therefore, relatedness between overlapping males and females may not underlie the mating system we have described. We suggest that the explanation may lie in multiple paternity and the reproductive biology of female American mink. Because female minks are capable of superfetation and are induced ovulators, an unguarded female has the opportunity to mate with any male she encounters during the mating season. In ranched animals, ≥ 4 waves of follicles mature at approximately 8-day intervals during the mating season (Sundqvist et al. 1988), although the maximum number of times a female can ovulate after successful matings is unknown. Also, the reported order effects (Shackelford 1952; Venge 1973) suggest that matings during the earlier mating season result in few kits. Therefore, a male seeking to ensure to sire any proportion of a litter might have to guard the mated female for ≥ 1 month. The dispersed spacing pattern of female minks (Birks 1981; Gerell 1970; Ireland 1988) may make this impractical for >1 female. In general, male mammals associating with certain females either socially or spatially try to guard, or conceal, those females from other males (Brotherton and Manser 1997; Jennions 1997). American mink, however, have a highly synchronized mating season with females capable of superfetation, and occupying predictable ranges—near water sources. Guarding even 1 female may not be easy—indeed, our results do not support the territorial precedence hypothesis, although the results are obviously based on partial litters except for F10. Under this circumstance, the roam-and-mate tactic may be more profitable for males than stay-and-guard within their territories. However, because female minks are capable of superfecundation, short term (2–3 days) mate guarding

might be expected especially toward the end of the mating season.

Our results also provide scant support for the investment protection hypothesis, as this was compatible with only 1 case out of 15 male–female combinations—although we are uncertain what proportion of nonreturning males (and pregnant females) had died. Our results, along with studies of ranched mink, suggest that the entire litter is unlikely sired by a single male, and that a male's progeny are likely to be widely and sparsely dispersed: males M1, M8, and M9 appear to have sired parts of litters that were spatially widely separate (see Fig. 2; Table 2). Even assuming that these males had offspring only within the 24-km study area, to cover the territories of all mothers of his surviving kits, each male would need to keep a territory of about 10–12.5 km along the river, which is almost twice as long as an average male territory size (6.8 km). Furthermore, even if a male sired part of a litter (5–8—Dunstone 1993), this may not guarantee the male that the surviving kits (2.5 just before they disperse—Dunstone 1993) include his, for which he may be providing the protection. Therefore, it may not be worthwhile for a male mink to settle in any particular area for providing protection to a female and her litter. In contrast, a male European pine marten is thought to settle in the territory of a female bearing his offspring, thereby excluding threatening rival males (Schröpfer et al. 1997). Presumably mixed paternity is less common in pine marten than in American mink. Indeed, superfetation, which facilitates multiple paternity, may not occur in the genus *Martes* (Mead 1994).

Delayed implantation and female reproductive tactics.—Several advantages of female multiple mating have been suggested in terms of female's reproductive fitness, such as fertilization assurance, mate retention, obtaining good genes, and increasing the genetic diversity of the litter (Arnqvist and Nilsson 2000; Jennions 1997; Jennions and Petrie 2000; Reynolds 1996). A female may be able to achieve polyandry more successfully by prolonging the window of opportunity for mating, both to increase access to more males and to diminish

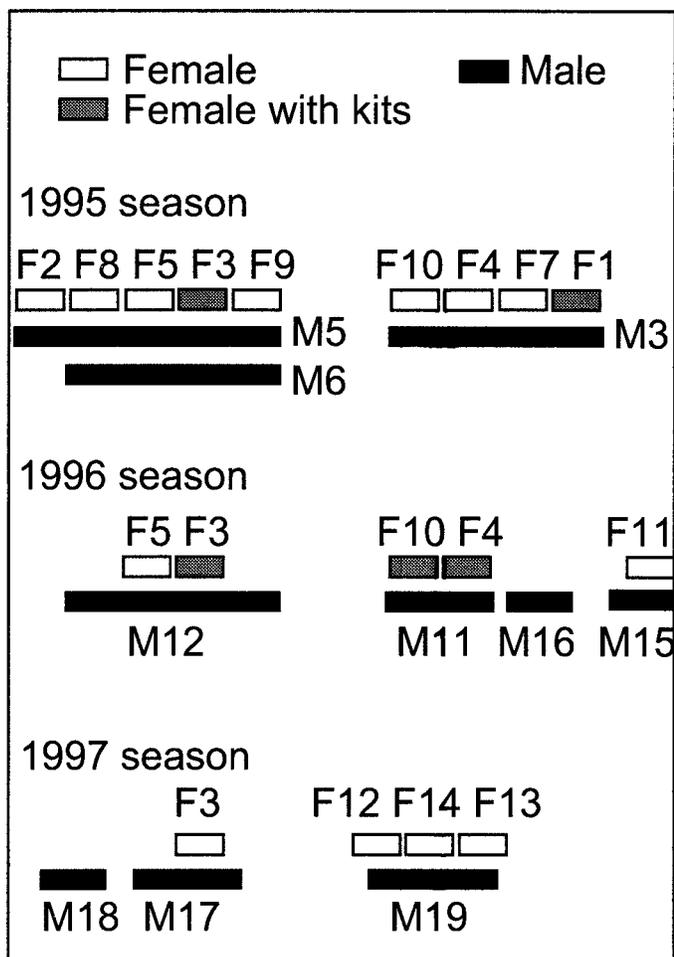


FIG. 3.—Range overlap between resident adult males and resident adult females, roughly corresponding to spatial position of each territory from upstream (left) to downstream (right). Note that female ranges are shown as mutually exclusive same-sized blocks for convenience. Each season starts in March and ends in February. Females F1 and F3 had kits in the 1995 season and F3, F4, and F10 in the 1996 season.

the chance of any one male securing a monopoly. In mink, superfecundation provides a mechanism whereby a female can avoid devoting her entire reproductive effort to 1 male. However, the chance of securing multiple fathers in 1 ovulation event is restricted to the 1–3 days following the first mating (Venge 1973). During this short period, it might indeed be feasible for 1 male to monopolize the female. The female's window of opportunity is greatly extended by superfetation. Endocrinological studies suggest that delayed implantation is a prerequisite for superfetation in American mink. Following the initial fertilization, the corpora lutea of mink do not initially produce sufficient quantities of progesterone to induce implantation, and this low level of progesterone is needed for the later estrus and ovulations (Sundqvist et al. 1988). This embryonic diapause is later terminated by the reactivation of corpora lutea and the following increase of their progesterone secretion, which is stimulated by prolactin from the pituitary (Martinet et al. 1981; Douglas et al. 1998). From this stage

onward, female minks do not ovulate as the ova are implanted and true pregnancy begins (Sundqvist et al. 1988). Therefore, without delayed implantation, superfetation cannot occur physiologically. This may suggest that the main functional advantage of the short delayed implantation in American mink is to enable a female to exhibit superfetation, which in turn gives her greater opportunities for multiple mating or polyandry, leading to enhanced reproductive fitness. Currently, mainstream hypotheses for the evolution of delayed implantation deals principally with how delayed implantation, once it exists, fine tunes mating and parturition times, and not with the origin of delayed implantation (C. M. King and R. A. Powell, in litt.). This short delay associated with superfetation may explain a possible origin of delayed implantation, and longer delays may have evolved thereafter.

Conclusion.—Our findings are consistent with the hypothesis that male minks relinquish their territories during the breeding season in response to the reproductive biology of female minks. The reproductive biology of female minks, especially the brief delayed implantation, may be a mechanism for increasing the extent of polyandry by prolonging the window of mating opportunity by superfetation. Males respond by adopting a roam-and-mate tactic. Further study is needed to test this mink model, disarticulating residency from fatherhood as well as a breakdown in residency during the mating season, and to determine if this phenomenon occurs broadly across other mustelids.

ACKNOWLEDGMENTS

We thank M. O'Connell for providing us mink microsatellite primers and P. Sherman, J. Wolff, J. Birks, M. Thom, D. Johnson, and B. Sheldon for their comments. This work was supported by grants to D. W. Macdonald by the Environment Agency and People's Trust for Endangered Species, and by the Overseas Research Student Award and the New Century Scholarship to N. Yamaguchi. This project was carried out under United Kingdom Home Office Personal License (PIL 30/3765) and Project License (PPL 30/1216). We also followed ASM guidelines for animal care and use (Animal Care and Use Committee 1998) throughout the study.

LITERATURE CITED

- ANDELMAN, S. J. 1986. Ecological and social determinants of cercopithecine mating patterns. Pp. 201–216 in *Ecological aspects of social evolution: birds and mammals* (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- ARMITAGE, K. B. 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies. Pp. 303–331 in *Ecological aspects of social evolution: birds and mammals* (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey.
- ARNQVIST, G., AND T. NILSSON. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* 60:145–164.

- BAILEY, T. N., E. E. BANGS, M. F. PORTNER, J. C. MALLOY, AND R. J. MCAVINCHIEY. 1986. An apparent overexploited lynx population on the Kenai peninsula, Alaska. *Journal of Wildlife Management* 50:279–290.
- BEN-DAVID, M. 1998. Delayed implantation in the marbled polecat, *Vormela peregusna sylvatica* (Carnivora, Mustelidae): evidence from mating, parturition, and post-natal growth. *Mammalia* 62: 269–283.
- BIRKS, J. D. S. 1981. Home range and territorial behaviour of the feral mink (*Mustela vison* Schreber) in Devon. Ph. D. dissertation, Exeter University, Exeter, United Kingdom.
- BIRKS, J. D. S., AND I. J. LINN. 1982. Studies on the home range of feral mink (*Mustela vison*). *Symposia of the Zoological Society of London* 49:231–257.
- BONESI, L. 1996. Spatial organisation and feeding ecology of the American mink (*Mustela vison*) in a coastal habitat. M.Sc. thesis, University of Durham, Durham, United Kingdom.
- BROTHERTON, P. N. M., AND M. B. MANSER. 1997. Female dispersion and the evolution of monogamy in the dik-dik. *Animal Behaviour* 54:1413–1424.
- CAILLOL, M., M. MONDAIN-MONVAL, AND B. ROSSANO. 1991. Gonadotrophins and sex steroids during pregnancy and natural superfetation in captive brown hares (*Lepus europaeus*). *Journal of Reproduction and Fertility* 92:299–306.
- DOUGLAS, D. A., A. HOUDE, J. H. SONG, R. FAROOKHI, P. W. CONCANNON, AND B. D. MURPHY. 1998. Luteotropic hormone receptors in the ovary of the mink (*Mustela vison*) during delayed implantation and early-postimplantation gestation. *Biology of Reproduction* 59:571–578.
- DUNSTONE, N. 1993. The mink. T and A D Poyser Ltd., London, United Kingdom.
- DURBIN, L. S. 1998. Habitat selection by five otters *Lutra lutra* in rivers of northern Scotland. *Journal of Zoology* 245:85–92.
- ERLINGE, S., AND M. SANDELL. 1986. Seasonal changes in the social organisation of male stoats, *Mustela erminea*: an effect of shifts between two decisive resources. *Oikos* 47:57–62.
- GERELL, R. 1970. Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. *Oikos* 21:160–173.
- GOUAT, J. 1985. Notes sur la reproduction de *Ctenodactylus gundi* rongeur Ctenodactylidae. *Zeitschrift für Säugetierkunde* 50:285–293.
- HATLER, D. F. 1976. The coastal mink on Vancouver Island, British Columbia. Ph. D. dissertation, University of British Columbia, Vancouver, Canada.
- HENZI, S. P., J. E. LYCETT, AND T. WEINGRILL. 1998. Mate guarding and risk assessment by male mountain baboons during inter-troop encounters. *Animal Behaviour* 55:1421–1428.
- IRELAND, M. C. 1988. The behaviour and ecology of the American mink (*Mustela vison* Schreber) in a coastal habitat. Ph.D. dissertation, Durham University, Durham, United Kingdom.
- JENNIONS, M. D. 1997. Female promiscuity and genetic incompatibility. *Trends in Ecology and Evolution* 12:251–253.
- JENNIONS, M. D., AND M. PETRIE. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* 75:21–64.
- JOHNSON, D. D. P., D. W. MACDONALD, AND A. J. DICKMAN. 2001. An analysis and review of models of the sociobiology of the Mustelidae. *Mammal Review* 30:171–196.
- KOMDEUR, J., F. KRAAIJEVELD-SMITH, K. KRAAIJEVELD, AND P. EDELAAR. 1999. Explicit experimental evidence for the role of mate guarding in minimising loss of paternity in the Seychelles warbler. *Proceedings of the Royal Society of London, B. Biological Sciences* 266:2075–2081.
- MACDONALD, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379–384.
- MARSHALL, T. C., J. SLATE, E. B. KRUK, AND J. M. PEMBERTON. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* 7:639–655.
- MARTINET, L., C. ALLAIS, AND D. ALLAIN. 1981. The role of prolactin and LH in luteal function and blastocyst growth in mink (*Mustela vison*). *Journal of Reproduction and Fertility Supplement* 29: 119–130.
- MEAD, R. A. 1981. Delayed implantation in mustelids, with special emphasis on the spotted skunk. *Journal of Reproduction and Fertility Supplement* 29:11–24.
- MEAD, R. A. 1993. Embryonic diapause in vertebrates. *Journal of Experimental Zoology* 266:629–641.
- MEAD, R. A. 1994. Reproduction in *Martes*. Pp. 404–422 in Martens, sables, and fishers biology and conservation (S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds.). Cornell University Press, Ithaca, New York.
- O'CONNELL, M., J. M. WRIGHT, AND A. FARID. 1996. Development of PCR primers for nine polymorphic American mink *Mustela vison* microsatellite loci. *Molecular Ecology* 5:311–312.
- PACKER, C., ET AL. 1988. Reproductive success of lions. Pp. 363–383 in *Reproductive success studies of individual variation in contrasting breeding systems* (T. H. Clutton-Brock, ed.). University of Chicago Press, Chicago, Illinois.
- POWELL, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Zeitschrift für Tierpsychologie* 50:153–165.
- POWELL, R. A. 1994. Structure and spacing of *Martes* populations. Pp. 101–121 in Martens, sables, and fishers: biology and conservation (S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds.). Cornell University Press, Ithaca, New York.
- REYNOLDS, J. D. 1996. Animal breeding systems. *Trends in Ecology and Evolution* 11:68–72.
- ROBITAILLE, J. F., AND M. RAYMOND. 1995. Spacing patterns of ermine, *Mustela erminea* L., in a Quebec agrosystem. *Canadian Journal of Zoology* 73:1827–1834.
- SAMBROOK, J., E. FRITSCH, AND T. MANIATIS. 1989. *Molecular cloning: a laboratory manual*. Cold Spring Harbor Laboratory Press, New York.
- SANDELL, M. 1986. Movement patterns of male stoats, *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. Pp. 164–182 in *Carnivore behaviour, ecology, and evolution* (J. L. Gittleman, ed.). Chapman and Hall, London, United Kingdom.
- SANDELL, M. 1990. The evolution of seasonal delayed implantation. *Quarterly Review of Biology* 65:23–42.
- SCHRÖPFER, R., P. WIEGAND, AND H.-H. HOGREFE. 1997. The implications of territoriality for the social system of the European pine marten *Martes martes* (L., 1758). *Zeitschrift für Säugetierkunde* 62:209–218.
- SHACKELFORD, R. M. 1952. Superfetation in the ranch mink. *American Naturalist* 86:311–319.
- SHERMAN, P. W. 1989. Mate guarding as paternity insurance in Idaho ground squirrels. *Nature* 338:418–420.
- SUNDQVIST, C., L. C. ELLIS, AND A. BARTKE. 1988. Reproductive endocrinology of the mink (*Mustela vison*). *Endocrine Reviews* 9:247–266.

- TAUSON, A. H., H. GUSTAFSSON, AND I. JONES. 1988. Flushing of mink. *Acta Agriculturae Scandinavica* 38:421–432.
- TAYLOR, M. E., AND N. ABREY. 1982. Marten, *Martes americana*, movements and habitat use in Algonquin Provincial Park, Ontario. *Canadian Field-Naturalist* 96:439–447.
- VENGE, O. 1973. Reproduction in the mink. Royal Veterinary and Agricultural University, Copenhagen, Denmark, Yearbook 1973: 95–146.
- WEIR, B. J. 1974. Reproductive characteristics of hystricomorph rodents. *Symposia of the Zoological Society of London* 34:265–301.
- WRANGHAM, R. W., AND D. I. RUBENSTEIN. 1986. Social evolution in birds and mammals. Pp. 452–470 in *Ecological aspects of social evolution: birds and mammals* (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey.
- YAMAGUCHI, N., AND D. W. MACDONALD. 2003. The burden of co-occupancy: intraspecific resource competition and spacing patterns in American mink, *Mustela vison*. *Journal of Mammalogy* 84: 1341–1355.

Submitted 6 January 2003. Accepted 15 April 2003.

Associate Editor was Nancy G. Solomon.