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Reproduction and natality of wolverine (*Gulo gulo*) in Yukon

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In Yukon, female wolverine did not breed as young of year and only 7% of subadults were pregnant. Of the adult females, 53% of 2+ year-olds were pregnant or post-partum and between 62% and 92% of 3+ year-old and older wolverine were pregnant or post-partum. The mean *in utero* litter size was 3.2 ± 0.8 *SD* ($n = 22$). Natality increased with age, ranging from a mean of 2.8 to 3.4 fetuses per adult female. Pregnant females were caught in all months of the trapping season (1 November to 31 March) indicating implantation occurred at least as early as November. Males were sexually mature by 2+ years of age. Bacula length and weight should not be used as criteria of age without other evidence.

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1. Introduction

Wolverine, like many of the Mustelidae, have delayed implantation (Wright & Rausch 1955). Breeding is thought to occur between April and October but primarily in mid-summer (Wright & Rausch 1955). Wolverine have bred in captivity during May (Mehrer 1976) and July (Mohr 1938), and in the wild during June (Krott & Gardner 1985) and August (Magoun & Valkenburg 1983). Implantation of blastocysts occurs from December through March (Rausch & Pearson 1972). Birth of 2 to 4 kits occurs in late winter and spring (Wright and Rausch 1955, Rausch & Pearson 1972, Liskop et al. 1981).

Knowledge of reproduction is central to population dynamics of wolverine and essential for determining timing and rates of harvest in Yukon. Our objectives were: to determine when proestrus, implantation, and parturition ocurs; to determine age of sexual maturity for males and females; and to estimate age-specific natality. Age-related characteristics of the baculum have been used to distinguish young from adult mustelids (King 1980). Wolverine are difficult to age (Banci 1982) and our large sample presented an opportunity to investigate the utility of bacula for aging male wolverine.

2. Methods

Wolverine carcasses were obtained from trappers in Yukon over 3 winters, 1982–83 to 1984–85. The trapping season in Yukon extends from 1 November to 31 March and our description of reproduction is limited to this period. Two upper premolars were processed for each carcass. If upper premolars were unavailable, lower premolars or canines were used. Teeth were decalcified, sectioned at 10 microns using a freezing microtome, and stained with Tolulene Blue. Ages were determined from annuli and age class was estimated using skull characteristics. Because young wolverine are born during late winter through summer, age at capture of young of year in winter will be about 0.5 years. Consequently, ages are presented as 0+, 1+, 2+, and so on. We classed age 0+ as "young of year", 1+ as "subadult" and 2+ and older as "adult".

Usable specimens consisted of 168 female reproductive tracts, 199 testes pairs, and 194 bacula. Difficulties in aging reduced these sample sizes for some analyses. For females, reproductive tracts were removed and frozen whole. Tracts were thawed and ovaries sliced longitudinally in 1 mm sections under a dissecting microscope. Corpora lutea were counted and the presence of developing follicles recorded. Corpora lutea regress rapidly after parturition (Rausch & Pearson 1972) and are an exact count of the number of ova shed for the most recent litter.

General characteristics of uteri were noted (not bred, thickened walls, flaccid). An attempt was made to flush uterine horns for blastocysts (Hamilton & Cook 1955) but few blastocysts were recovered and the technique was abandoned. Flushing does not appear to be a reliable technique for the recovery of

Table 1. Reproduction of female wolverine from Yukon 1982–1985. For adult females (2+ or older) corpora lutea were determined from pregnant or post-partum wolverine.

Age	*n*	% pregnant or post partum	Corpora lutea *n*	Corpora lutea mean±*SD*	Estimated[a] fetuses
0+	62	0.0	62	0.0±0.0	0.0
1+	27	7.4	27	0.2±0.8	0.2
2+	30	53.3	15	3.1±0.8	2.8
3+	13	92.3	10	3.6±0.7	3.1
4+	13	92.3	10	4.1±1.0	3.4
5+	7	85.7	6	4.2±0.8	3.4
6+–11+	8	62.5	5	4.4±1.1	3.4

[a] Linear interpolation using known relationship between number of corpora lutea and mean number of fetuses for females having in utero litters.

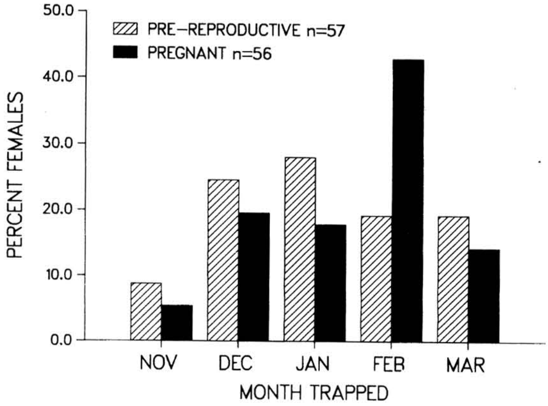

Fig. 1. Pre-reproductive and pregnant wolverine trapped November to March, Yukon 1982–1985.

blastocysts because loss rate is high (Rausch & Pearson 1972, Liskop et al. 1981). In addition, carcasses were in varying stages of decomposition and the condition of the blastocysts was questionable. Uterine horns were slit longitudinally and examined for placental scars. Regression of placental scars is relatively rapid (Rausch & Pearson 1972), therefore counts are not biased by scars from previous litters. If females were macroscopically pregnant, fetuses were removed, weighed and crown-rump length measured. Females were classified as: non-reproductive (no corpora lutea, no developing follicles, no placental scars); pre-reproductive (developing follicles present in ovaries); pregnant (corpora lutea, implantation sites or fetuses present); post-partum (degenerating corpora lutea, fading scars, flaccid reproductive tract).

The relationship between mean number of fetuses and number of corpora lutea was examined for females having macroscopic embryos. Mean number of corpora lutea was calculated for each age class of females. Number of fetuses was estimated by linear interpolation between 2 data points of the known relationship between corpora lutea and fetuses. Mean numbers of corpora lutea, scars and fetuses were compared using t-tests.

Paired testes and epididymides were weighed. If only one testis was present, the weight of the pair was estimated by doubling the weight of the single testis. Carcasses were subject to varying degrees of dessication. Testes, being externally situated, were especially susceptible to drying. Because dessication was not consistent, weights were standardized by soaking testes in water for 24 hours. Bacula were stripped of flesh, cleaned by dermestid beetles and weighed. Maximum length was measured using dial calipers. Atypical bacula, those broken and rehealed in bent positions, were omitted. Oneway ANOVA to test for significance followed by multiple comparisons using Fisher's Modified Least Significant Difference were used to compare testes weights, bacula weight and bacula length among age classes. ANOVA was used to examine variation in mean weights of testes by age class and time of year. Means ± 1 standard deviation are reported.

3. Results

3.1. Females

Young of year females were either non-reproductive (21 of 62) or pre-reproductive (41 of 62) and 7% of subadults (2 of 27) were pregnant. The percent of females pregnant or post-partum was 73% (58 of 79) but varied by age (Table 1). Pregnant females were caught throughout the trapping season (Fig. 1), indicating implantation occurred at least as early as November. The variability of fetus crown-rump length (Fig. 2) suggests an extended period of implantation and subsequently, parturition. A female caught on 3 March was near term; the fully furred fetuses (n = 4) had a mean weight of 107.7 g and mean crown-rump length of 112.5 mm. In contrast, fetuses (*n* = 4) of a female trapped on 15 March had mean weights of 7.1 g and a mean crown-rump length of 53.0 mm. Of post-partum females (*n* = 7), 1 was captured in January and 5 in February. One post-partum female captured on 8 November had placental scars but no corpora lutea, indicating either a late birth or that absorbtion of embryos had occurred. Developing follicles as well as regressing corpora lutea were present in ovaries of all post-partum females.

Mean number of corpora lutea increased with age to a maximum of 4.4 ± 1.1 (Table 1). The smallest number of corpora lutea for pregnant females was 2. For 23 females with macroscopic embryos, mean number of corpora lutea (3.9 ± 1.0) overestimates

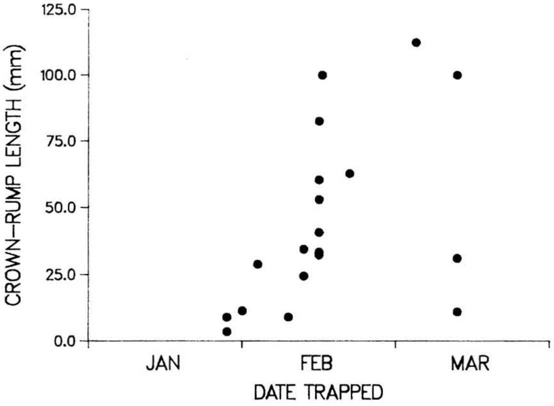

Fig. 2. Mean crown-rump length for *in utero* litters of wolverine trapped January to March, Yukon 1982–1985.

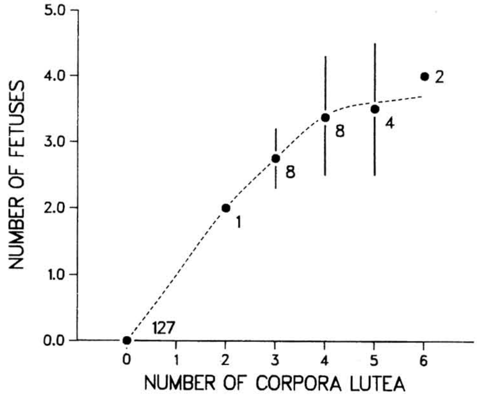

Fig. 3. Mean number of wolverine fetuses observed and number of corpora lutea, Yukon 1982–1985. Standard deviations and sample sizes are indicated.

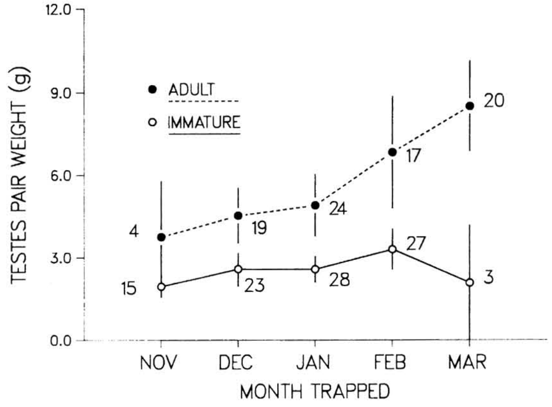

Fig. 4. Mean weights of testes pairs for age classes of wolverine trapped November through March, Yukon 1982–1985. Weights were standardized by soaking testes in water for 24 h. Standard deviations and sample sizes are indicated.

mean number of fetuses observed (3.2 ± 0.8) (paired $t_{22} = 3.87$, $P < 0.01$). However, mean number of placental scars (3.3 ± 1.2, $n = 18$) did not differ from mean number of fetuses, ($t_{40} = 0.36$, $P > 0.70$). Neither counts of placental scars nor fetuses take into account embryos that are absorbed or young that die after birth. Of 19 litters having measurable fetuses, 1 fetus from a litter of 3 and 1 from a litter of 4 were beginning to disintegrate in the uterus.

For 23 females with macroscopic embryos, the number of corpora lutea is related to mean nmber of fetuses (Fig. 3). Using this relationship and mean counts of corpora lutea, number of fetuses was estimated for females of each age class (Table 1). The following assumptions were made in these calculations: a 1:1 relationship for $n \leq 2$ corpora lutea and fetuses; because only a small proportion of subadults reproduce, the estimated number of fetuses for this age class is the observed proportion; because the potential number of young mature females is capable of producing is independent of whether or not she becomes pregnant, mean corpora lutea counts include only adult females which were pregnant or post-partum.

3.2. Males

Oneway ANOVA indicated mean weights of testes differed among age classes of wolverine ($F_{2,196} = 44.96$, $P < 0.01$). However, mean testes weights of subadults did not differ from young of year ($P > 0.05$) and these age classes are considered as "immature". Age class and month trapped were significant factors in explaining variation in male testes weights ($P < 0.01$). Testes weights of adults increased in February and March (Fig. 4). Differences existed between age classes in mean length ($F_{2,191} = 39.78$, $P < 0.01$) and weight ($F_{2,191} = 61.28$, $P < 0.01$) of bacula. However, overlap of these measurements indicate age classifications based on characteristics of bacula are not definitive (Table 2).

Table 2. Bacula measurements for age classes of Yukon wolverine, 1982–1985.

Age class	*n*	Length (mm)				Weight (g)			
		mean±*SD*	min	max	95% conf. lim.	mean±*SD*	min	max	95% conf. lim.
Young of year	61	73.30±5.07	58.06	84.04	72.04–74.64	1.06±0.31	0.59	2.13	0.98–1.14
Subadult	40	76.19±6.18	62.12	88.40	74.22–78.17	1.28±0.50	0.63	3.13	1.12–1.45
Adult	93	81.05±5.18	56.82	91.72	79.98–82.12	1.96±0.62	0.82	3.35	1.83–2.09

4. Discussion

4.1. Females

Pre-reproductive females were trapped in all months from November through March and the proestrus period could not be determined for wolverine. Induced ovulation is common in mustelids and occurs in mink (*Mustela vison*) and ermine (*Mustela erminea*) (Martinet et al. 1984), polecat (*Mustela putorius*) and skunk (*Mephitis mephitis*) (Mead & Wright 1983), and likely occurs in wolverine. The prolonged estrus characteristic of induced ovulators is usually effected by growth of several follicular waves (Weir & Rowlands 1973). Because many follicles develop but only few actually ovulate (Weir & Rowlands 1973), presence of follicles in ovaries or time of development cannot be construed as evidence that estrus is pre-eminent.

Female wolverine in Yukon did not breed in their first summer and our results are consistent with results of Rausch and Pearson (1972) and Liskop et al. (1981). Of subadults, 7.4% were pregnant, in contrast with the 50.0% (20/40) reported by Rausch & Pearson (1972) and 84.6% (11/13) reported by Liskop et al. (1981). Direct comparison with Rausch & Pearson (1972) is difficult as they classified young of year as "0–15 months" and subadults "16–28 months". Both Rausch & Pearson (1972) and Liskop et al. (1981) used cementum analysis as an aging technique. Wolverine are difficult to age using this method (Banci 1982) and error in reported ages should be considered. However, even assuming that a proportion of subadults were misclassified by age, pregnancy rate for subadult females in our study is the lowest reported for wolverine. Approximately 50% of the 2+ age class were pregnant. Because Rausch & Pearson (1972) and Liskop et al. (1981) lumped 2+ year-old and older females into "adults", age specific comparisons cannot be made. Age of sexual maturity in mustelids varies with nutrition (Mead & Wright 1983). Differences in age of sexual maturity between Yukon (1982–1985) and other areas and periods may reflect differences in nutrition status.

Although methodological differences make some comparisons with other studies difficult, results from mature females imply that differences in reproductive rates exist among wolverine populations. The proportion of adult females pregnant (73.4%) in our sample is less than that found in Alaska and Yukon, 91.8% (90/98) (Rausch & Pearson 1972), and in British Columbia, 88.5% (23/26) (Liskop et al. 1981). Comparison of reproductive rates of wolverine among studies using corpora lutea counts is not possible because the authors did not state whether they included ovaries with no corpora lutea in their calculations. In addition, the utility of this statistic is limited without considering age-specific differences. Rausch & Pearson (1972) found no difference in number of ova shed between first breeders and multiparous females. Our results indicate that reproductive rate increases with age, consistent with age-specific natality described for other mammals (Caughley 1977:83). Because reproduction is age-dependent, differing age compositions of samples between studies could account for some of the differences in estimates of natality.

Unimplanted blastocysts have been found in females killed in October, November and January (Wright & Rausch 1955); in December (Rausch & Pearson 1972); and in February and March (Liskop et al. (1981)). In our sample, pregnant females occurred in all months of the trapping season and indicates that time of implantation occurs at least as early as November. The variation of embryo size emphasizes the variability in timing of implantation and parturition. If a female implants in November, and the active period of pregnancy is 30 to 40 days (Rausch & Pearson 1972), birth would occur in December. This may be an inhospitable time to give birth for many northern mammals but not necessarily for wolverine. Parturition should be timed for maximum survival of young, likely the time of greatest food availability. Because wolverine are scavengers dependent on ungulate carcasses, food should be more plentiful in winter, and this may be the best season for wolverine reproduction.

Non-pregnant females occurred in sexually mature age classes of wolverine. The proportion of non-pregnant females in age classes 2+ to 5+ years ranged from 7.7 to 46.7%. Pregnancy rate of females 6+ years and older (62.5%) may be less than that of younger adults. This estimate needs to be confirmed with a larger sample size. The relatively high proportion of pregnant adults (73.4%) indicates that most females breed annually, presumably even if they have had a litter the same year. In many mammals, ovulation occurs shortly after parturition (Weir & Rowlands 1973). The presence of follicles in ovaries of post-partum females suggests wolverine females are capable of breeding soon after having young. Reproductive characteristics and success are closely linked to food resources (Robbins 1983:167–206). However, the relationship between habitat productivity and wolverine reproduction is not clear. The oldest female in our study with no evidence of prior breeding was 4+ years. Female wolverine in arctic Alaska that inhabited an area where food was scarce bred but not all produced kits (Magoun 1985). One adult female produced no young in the 3 years she was observed (Magoun 1985). Approximately 50% of monitored females in an area having greater food resources were not pregnant (Hornocker & Hash 1981). Two of 3 radio-collared adult females in Yukon where food was apparently abundant did not reproduce (Banci 1987).

Newborn wolverine kits are altricial (Shilo & Tamarovskaya 1981). By 7 months of age, kits in the wild attain adult weight (Magoun 1985). Rapid growth of young emphasizes the large energy and nutrient contribution made by their mothers. Lactation is energetically very expensive, more so than gestation (Sadleir 1984). Even if a female with kits does breed, such demands may influence her ability to reproduce the following year. Evidence from radio-collared wolverine suggests the proportion of females pregnant determined from reproductive tracts overestimates the proportion of females in the population that will have young. Loss of young may occur before or after birth. Absorbtion of fetuses was observed for 2 of 19 macroscopic *in utero* litters. The proportion of non-detectable losses *in utero* is unknown but likely large, considering the low reproductive success observed in the wild. Loss after parturition (1 kit each from 2 litters of 4) was reported by Pulliainen (1968). The relatively high proportion of adult females pregnant in our study and that found by Rausch & Pearson (1972) and Liskop et al. (1981) suggest reproductive losses occur primarily *in utero* and after implantation. The condition of females before implantation may be the most critical factor determining reproductive success.

Mean litter size from *in utero* fetuses in our study (3.2) exceeds that reported for northern British Columbia (2.6) (Liskop et al. 1981) and is comparable to that reported for Alaska and Yukon (3.5) (Rausch & Pearson 1972). The value for northern British Columbia is based on 5 females and may be inaccurate because of the small sample size. Rausch & Pearson (1972) report a range of 1 to 6 "detectable" fetuses ($n = 54$ females). Their plot of crown-rump length over time is based on a smaller sample ($n = 20$ fetuses) and implies "detectable" fetuses includes those that were too small to be easily measured. This range includes fetuses which would be absorbed early and is an overestimate of actual number produced. *In utero* litters in our study ranged from 2 to 4 kits. From 161 dens in Finland, Pulliainen (1968) reported a mean litter size of 2.5, litters of 2 and 4 were rare. In arctic Alaska, from 5 litters a maximum of 2 kits were observed after den abandonment (Magoun 1985).

4.2. Males

Based on evidence of spermatogenesis, Liskop et al. (1981) classified males as mature if testes weighed more than 6.5 g. Using this criterion, in Yukon no subadults were sexually mature, whereas by March all adults were in breeding condition. Rausch & Pearson (1972) noted males were sexually mature at 14–15 months but some did not show evidence of spermatogenesis until 26–27 months. Our results indicate most males, as most females, are not reproductively active until 2+ years of age. Rausch & Pearson (1972) reported a peak in testes weights in June, presumably also indicating the peak in breeding activity. The trend of increase in average weight of testes during early spring is apparent in our data.

Growth of bacula is stimulated by male hormones at the onset of sexual maturity (Wright 1950). Rausch & Pearson (1972) commented on the overlap in bacula weights between age classes and concluded their utility was limited to separating young of year from older animals. Our results using both length and weight of bacula agree with their findings. Extent of overlap in bacula measurements between young of year and subadults supports an age at sexual maturity of 2+ years for male wolverine. Bacula measurements should not be used as criteria of age without other evidence.

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