SEX-SPECIFIC DISPERSAL PATTERNS OF WOLVERINES: INSIGHTS FROM MICROSATELLITE MARKERS

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Dispersal of individuals can be defined as movement and settling outside the natal home range. Such dispersal is often sex-biased among vertebrates, and is generally expected to be male-biased in polygynous mammals. We used microsatellite markers scored on harvested wolverines (*Gulo gulo*) to test the prediction of male-biased dispersal in a population in the western Brooks Range, Alaska. Our analyses suggested a high rate of dispersal within the population, but provided no support for sex differences in dispersal tendencies across the sampled spatial scale. Previous studies have implied male-biased dispersal among wolverine populations on an interpopulation scale. We suggest 3, not exclusive, explanations to reconcile these differences: low power to detect sex biases in dispersal tendencies in this panmictic population; a scale-dependent component in dispersal tendencies, where males are overrepresented among interpopulation migrants; and lower reproductive success for dispersing females compared to more philopatric ones.

Key words: carnivore, genetics, *Gulo gulo*, isolation by distance, mustelid, social structure, spatial patterns, wolverine

Individuals of many vertebrate species disperse from their natal home range (see Howard [1960] for definitions), with such natal dispersal often skewed toward individuals of one sex. Sexual asymmetry in dispersal rates and distances can have important ramifications for population demographics and may substantially affect effective population size, particularly for small and isolated populations (Hastings and Harrison 1994). Sex-biased dispersal also may impact metapopulation dynamics and persistence of subpopulations, because it dictates the level of gene flow between subpopulations (Hanski and Gilpin 1997). Therefore, estimates of relative dispersal rates between males and females are critical for several aspects of natural resource management, such as management of endangered populations (Waser et al. 2001).

Despite the frequent occurrence of sex-biased dispersal, its causes are often less obvious. Inbreeding avoidance (Pusey 1987), kin competition (Greenwood 1980; Hamilton and May 1977), and resource competition (Perrin and Mazalov 2000; Waser 1985) have been proposed as key factors. Although earlier theory identified specific factors that may drive the evolution of sex-biased dispersal (Shields 1987), recent models suggest that multiple factors interact in shaping dispersal patterns in animal populations (Gandon and Michalakis 2001; Perrin and Goudet 2001), a suggestion that is supported empirically (Lambin et al. 2001). Further, the factors influencing sex-biased dispersal may vary among populations within a species depending on local environmental conditions (Lidicker and Stenseth 1992).

In group-living mammalian carnivores, male-biased dispersal and female philopatry appear to be the general pattern (e.g., African lion, [*Panthera leo*—Packer and Pusey 1993] and gray wolf [*Canis lupus*—Peterson et al. 1984]), although exceptions with reversed bias exist (e.g., European badger [*Meles meles*—Woodroffe et al. 1993]). In solitary carnivores, male-biased dispersal is suspected for most species (Sandell 1989; Waser and Jones 1983), but empirical evidence is still sparse. However, long-term monitoring programs of known individuals have revealed male-biased dispersal in Bengal tigers (*Panthera tigris*—Smith and Macdougal 1991), Scandinavian and North American brown bears (*Ursus*
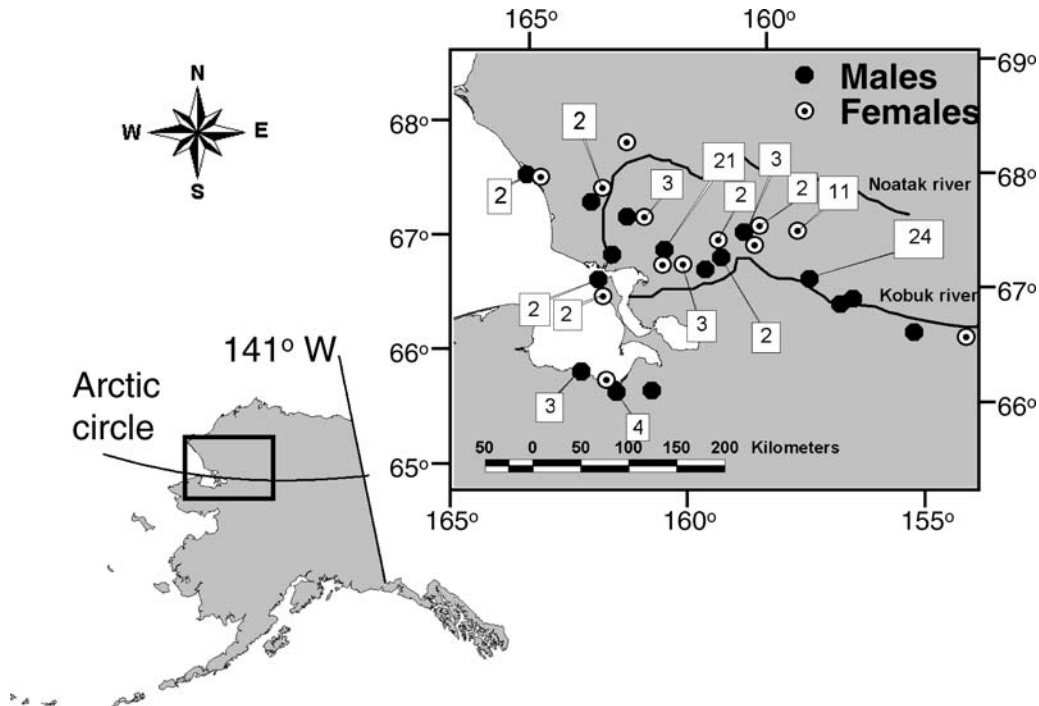

FIG. 1.—Locations of harvested wolverines included in the study. Number of animals harvested at a specific location ranged from 1 to 13 females and 1 to 23 males.

arctos—Paetkau et al. 1998; Swenson et al. 1998), and American black bears (*Ursus americanus*—Rogers 1987). Genetic methods have similarly been used to document male-biased dispersal in raccoons (*Procyon lotor*—Ratnayeke et al. 2002).

The wolverine (*Gulo gulo*) is a medium-sized, solitary carnivore with a circumpolar distribution in the arctic and boreal zones (Pasitschniak-Arts and Lariviere 1995). As in most solitary carnivores, dispersal of wolverines is generally assumed to be male-biased (Banci 1994). Direct observations of radio-tagged animals in Scandinavia suggested that males dispersed more frequently than females and that females delayed dispersal relative to males, but that males and females dispersed equal distances (Vangen et al. 2001). Although previous studies using genetic techniques on samples from multiple populations (Cegelski et al. 2003; Chappell et al. 2004; Kyle and Strobeck 2001, 2002; Tomasik and Cook 2005; Wilson et al. 2000) generally indicate male-biased dispersal on an inter-population scale, our knowledge of dispersal patterns within populations is still poor.

In this study, we used information from microsatellite markers to test the hypothesis of male-biased dispersal within a population of wolverines in the western part of the Brooks Range, Alaska. In contrast to previous studies using genetic markers on this species, we investigated dispersal patterns within a single population on a relatively small geographic scale.

MATERIALS AND METHODS

Sample collection.—We purchased carcasses of legally harvested wolverines from local hunters between 1996 and 2002. All wolverines were harvested within the Noatak and Kobuk river drainages in the western Brooks Range, Alaska (64°50′N–68°00′N, 155°W–165°W), except for 8 that were harvested on the northeastern part of the Seward Peninsula (Fig. 1). Hunters provided information on harvest locations, which ranged from accurate geographic coordinates to general locations described by the nearest hunting camp or village. The area covered by the sampling effort was approximately 80,000 km^2. Voucher specimens are deposited in the Mammal Collection at the University of Alaska Museum of the North, Fairbanks (Appendix I).

A canine tooth was extracted from harvested animals and was used for age determination (Matson Laboratory, Milltown, Montana—Matson 1981). Based on tooth annuli counts, we divided animals into 2 discrete age classes (i.e., <2 years and ≥2 years of age). Wolverines tend to disperse before 2 years of age (Vangen et al. 2001). Thus, animals older than 2 years should represent already dispersed individuals, whereas animals younger than 2 years of age may represent predispersal, postdispersal, or dispersing individuals. For our analyses, animals estimated as younger than 2 years were classed as subadults and animals estimated as 2 years or older were classed as adults.

DNA extraction and microsatellite analyses.—We extracted genomic DNA from muscle samples with chelex resin (Small et al. 1998) and amplified 10 microsatellite loci (Gg10, Gg25, Gg37, Gg42, Gg192, Gg443, Gg452, Gg454, Gg465, and Gg471; Table 1) using primers previously developed for wolverines (Walker et al. 2001). Polymerase chian reaction amplification was carried out in 10-μl reactions containing 25–50 ng of genomic DNA, 30 mM deoxynucleoside triphosphates,

TABLE 1.—Number of samples scored, number of alleles, allele length (base pairs), and observed (H_O) and expected (H_E) levels of heterozygosity for 10 microsatellite loci of wolverines from the western Brooks Range, Alaska. None of the 10 loci differ significantly from Hardy–Weinberg expectations, and there were no signs of linkage disequilibria.

| Locus	$n_{samples}$	$n_{alleles}$	Minimum length	Maximum length	H_O	H_E
Gg10	134	6	149	181	0.62	0.62
Gg25	142	6	155	167	0.48	0.47
Gg37	144	5	198	206	0.69	0.68
Gg42	144	5	194	202	0.61	0.62
Gg192	143	6	166	188	0.56	0.67
Gg443	145	6	86	96	0.52	0.56
Gg452	134	4	111	119	0.42	0.39
Gg454	144	9	118	136	0.64	0.67
Gg465	144	6	168	180	0.71	0.72
Gg471	145	3	106	114	0.21	0.22

FIG. 2.—Standardized assignment indexes (i.e., frequencies of AIc values divided by total number of animals of each sex and age class) for male and female wolverines estimated to be adults (≥ 2 years of age, $n = 14$ males and $n = 9$ females) and subadults (<2 years of age, $n = 70$ males and $n = 37$ females).

0.2 µM of each primer, $1\times$ polymerase chain reaction buffer, 0.125 U/µl *Taq* polymerase (Perkin-Elmer, Boston, Massachusetts), and 1.5 mM $MgCl_2$. Amplification conditions were as follows: 94°C (3 min), then 32 cycles of 94°C (30 s), 52°C (45 s), 72°C (75 s), with a final 30-min extension at 72°C. We analyzed amplified products using an ABI 3100 automated DNA sequencer (Applied Biosystems Inc., Foster City, California) and sized microsatellite alleles using an internal GS 350 ROX (Applied Biosystems Inc.) size standard. We used the software GeneScan 3.1 (Applied Biosystems Inc.) and Genotyper 2.1 (Applied Biosystems Inc.) to collect and analyze the microsatellite data.

Data analysis.—We calculated observed and expected levels of heterozygosity using GENEPOP, version 3.4 (Raymond and Rousset 1995), and tested for deviations from Hardy–Weinberg expectations using an exact test based on a Markov chain algorithm presented by Guo and Thompson (1992). We tested for linkage disequilibria using an exact test based on a Markov chain algorithm as implemented in GENEPOP. Significance levels for both tests were adjusted for multiple comparisons using the false discovery rate method (FDR; Benjamini and Hochberg 1995).

We explored potential population structure by estimating the number of subpopulations using the software Structure, version 2 (Pritchard et al. 2000). We tested potential number of subpopulations (K) ranging from 1 to 5. For each K, we performed 100,000 iterations after a burn-in period of 100,000 iterations. We repeated the simulations 5 times and used the average of the 5 runs to calculate posterior probabilities for each K.

We used 2 separate analyses to test for patterns related to sex-biased dispersal in our genetic data. First, we used an assignment-based approach 1st implemented by Favre et al. (1997). This method capitalizes on the fact that the alleles of dispersed individuals should be less common in the population in which they are found than the alleles of nondispersed individuals. The method estimates the probability that a specific genotype originated from the population in which it was sampled by calculating an assignment index for each individual. This index is based on the average allele frequency in each
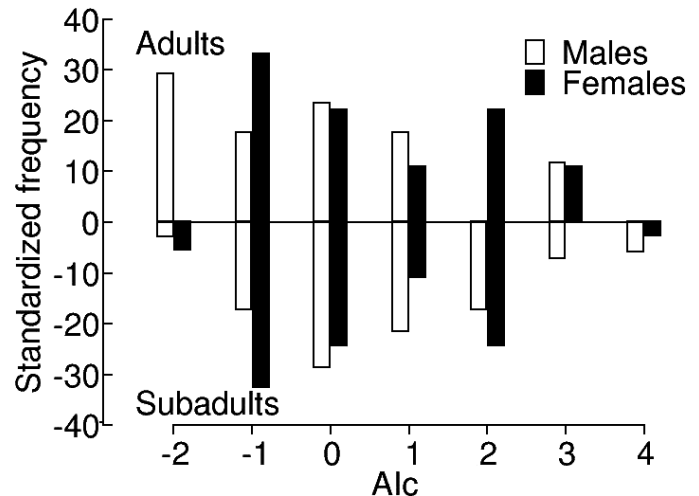
sampled population. Two specific predictions can be made regarding the distribution of assignment indexes in the case of sex-biased dispersal: assignment indexes should be negatively skewed for the dispersing sex; and the variance of assignment indexes should be higher for the dispersing sex.

We calculated an assignment index (AIc) for each individual using the software GeneClass2 (Piry et al. 2004). We assigned all individuals to one population. AIc values are presented as log-transformed normalized values (i.e., the population means were extracted from each log-transformed AIc value) as described by Favre et al. (1997). We have presented the results as standardized frequencies of animals within 8 discrete classes of AIc values. These standardized frequencies were calculated by dividing the raw frequencies of individuals within a given range of AIc values with the total number of individuals for that sex and age class. We tested if average assignment indexes varied between sexes and age classes using analysis of variance, including sex, age class, and an interaction term between sex and age class in the model. We tested for differences in variances of assignment indexes between sexes and age classes using multiple *F*-tests and inferred significance after adjusting for multiple comparisons using the FDR method.

The 2nd analysis we used to test for sex-biased dispersal relates pairwise estimates of genetic relatedness to pairwise geographic distances between individuals. If 1 sex disperses more frequently, and over longer distances, dyads of this sex should show a lower correlation between genetic relatedness and distance than the philopatric sex (Prugnolle and de Meeus 2002). We calculated pairwise coefficients of genetic relatedness with SPAGeDi, version 1.1 (Hardy and Vekemans 2000). We used the coefficient of genetic relatedness described by Wang (2002), which is a robust and unbiased estimator. We estimated pairwise geographic distances between harvest locations using ArcView software (ESRI, Redlands, California). However, because of the uncertainty in harvest locations for
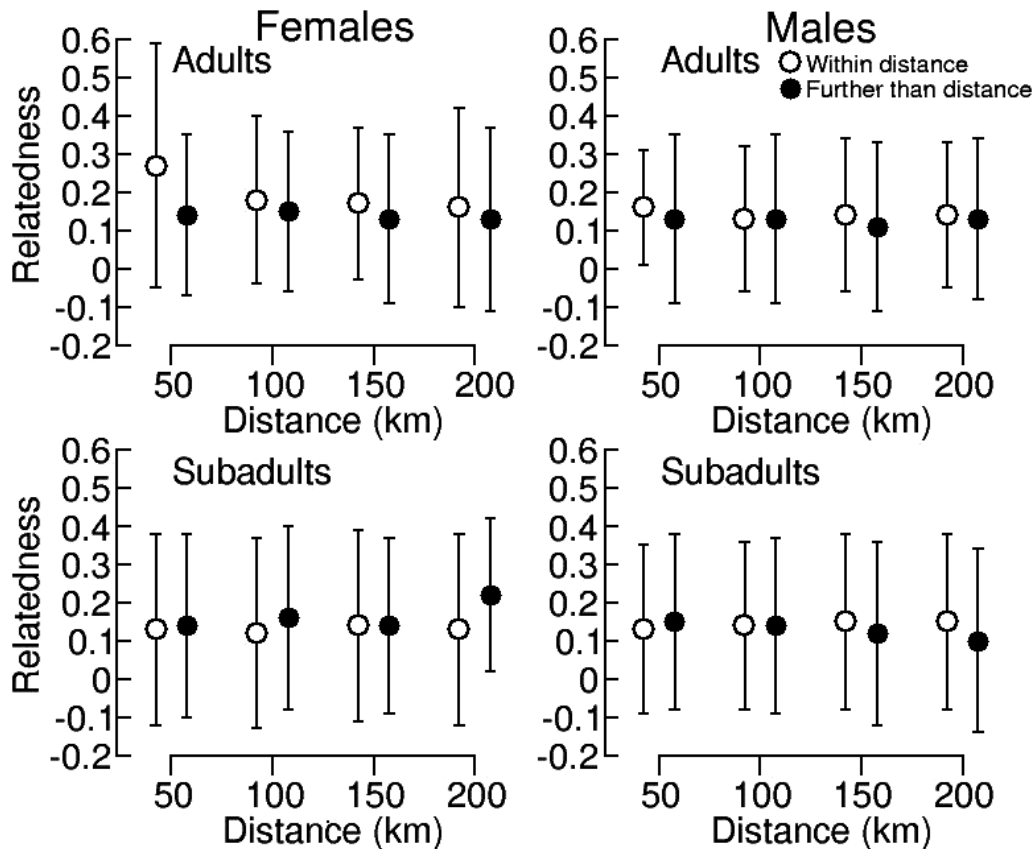
FIG. 3.—Relationships between pairwise coefficients of genetic relatedness and geographic distances between harvest locations for adult ($\geq$2 years) and subadult (<2 years) female and male wolverines. The graph show average relatedness ($\pm$ *SD*) between pairs of individuals harvested within (open dots) and farther than (solid dots) 4 specific distances, 50, 100, 150, and 200 km.

many individuals, we regarded distance as a discrete classification rather than a continuous variable, which is most common in these types of analyses (Prugnolle and de Meeus 2002). We classed the pairwise distances as either above or below specific distances set to 50, 100, 150, and 200 km. We used 50–200 km as demarcation points because these values reflect a realistic range of dispersal distances for wolverines (Vangen et al. 2001). We tested for differences in pairwise coefficients of relatedness between animals harvested less than and farther than 50, 100, 150, and 200 km apart by 2-sample permutation tests (R package exactRankTests v0.8.9, http://www.r-project.org). We conducted separate tests for dyads within each sex and age category and adjusted the *P*-values for multiple comparisons according to the FDR method. Statistical analyses were conducted using the statistical package R version 2.0 for Linux (http://www.r-project.org).

RESULTS

We scored 10 microsatellite loci in 145 wolverines, including 49 females, 91 males, and 5 of unknown sex. These 5 were used for descriptive statistics of the microsatellite data but were not included in the dispersal analyses. Nine of the 46 females for which we determined age and 14 of the 84 males were classed as adults. We had harvest locations for 107 animals, of which 9 were adult females, 28 were subadult

females, 1 was a female of unknown age, 10 were adult males, 55 were subadult males, and 4 were males of unknown age.

The average number of alleles per locus was 5.6 $\pm$ 1.58 *SD* and average expected heterozygosity was 56% $\pm$ 16% (Table 1). None of the 10 loci deviated significantly from Hardy–Weinberg expectations after adjusting for multiple comparisons, and there was no statistical evidence for linkage disequilibria.

The analyses using Structure revealed no detectable clusters within the population, with posterior probabilities below 10^{-15} for all *K* (i.e., number of clusters) from 2 to 5. Posterior probability for *K* = 1 was 1.

There were no differences in average assignment indices between males and females ($F = 0.61$, *d.f.* = 1,129, $P = 0.44$) or between subadult and adult individuals ($F = 0.32$, *d.f.* = 1, 129, $P = 0.57$; Fig. 2). Further, there was no significant interaction effect of sex and age on assignment indexes ($F = 0.52$, *d.f.* = 1, 129, $P = 0.47$), nor any differences in the variances of assignment indexes between any of the age classes within and between sexes ($P_{adj} > 0.95$ for all comparisons).

The average coefficient of relatedness calculated across all years and both sexes was 0.15 $\pm$ 0.24 *SD*. There were no significant differences in relatedness between individuals harvested within and further than either 50, 100, 150, or 200 km apart, either for subadult females ($P_{adj} = 0.35$–0.98), adult females ($P_{adj} = 0.98$), subadult males ($P_{adj} = 0.10$–0.98), or adult males ($P_{adj} = 0.98$; Fig. 3).

DISCUSSION

Expected heterozygosity in this population was similar to that of other high arctic populations, whereas number of alleles per locus appeared higher than that reported elsewhere (Kyle and Strobeck 2002). Higher gene flow between northern populations of wolverines when compared to southern populations (Kyle and Strobeck 2001, 2002; Wilson et al. 2000) has been attributed to fewer human-caused barriers to movement (Rowland et al. 2003; Tomasik and Cook 2005). Both the expected level of heterozygosity and the average number of alleles found in our population support this high connectivity among northern populations. Our failure to find subpopulation structure among our samples further indicates a high level of dispersal. In contrast, Wilson et al. (2000) found population differentiation among wolverines sampled only 100 km apart. However, Wilson et al. (2000) used maternally inherited mitochondrial DNA, which would be more likely to indicate population differentiation if females are more philopatric.

Although examination of our data suggested a high level of dispersal within the population, neither of our methods detected genetic patterns related to sex-biased dispersal. However, both theoretical (Goudet et al. 2002) and empirical (Cegelski et al. 2003) studies have indicated that average AIc values are less powerful than methods using genetic divergence (F_{st}) or relatedness values. Further, examination of our data indicates that the sampled animals belonged to a large panmictic population of wolverines. In such a situation, interpopulation migrants, the basis for assignment based approaches, might be difficult to detect. The approach using genetic relatedness should not be as adversely affected by panmixia as AIc values, and we suggest that our results reflect no or low sex-bias in dispersal tendencies across the sampled spatial scale.

Although Vangen et al. (2001) used radiotagged individuals to investigate wolverine dispersal on an intrapopulation level, studies that have addressed sex-biased dispersal using genetic techniques have exclusively looked at differences in interpopulation migration rates between males and females (Cegelski et al. 2003; Chapell et al. 2004; Flagstad et al 2004; Kyle and Strobeck 2001, 2002; Wilson et al. 2000). These studies generally indicate low population fragmentation using biparentally inherited markers, but substantial population differentiation using maternally inherited DNA (Tomasik and Cook 2005). This pattern is consistent with male-biased dispersal on an interpopulation scale (Slatkin 1987).

Thus, the contrast between these patterns and the present study could either be caused by a scale-dependent component in dispersal tendencies, where males tend to be overrepresented among interpopulation migrants, or by low power to detect sex-biased dispersal tendencies within this population. An alternative, but not exclusive, explanation could also be a strong negative skew in reproductive success for dispersing females. This could generate genetic patterns that indicate male-biased dispersal in markers that reflect a longer-term genetic history (e.g., mitochondrial DNA—Slatkin 1987), whereas contemporary genetic markers (e.g., microsatellites) and direct observations of individuals would not.

To conclude, examination of our data supports high rates of dispersal among individuals in this wolverine population, but we found no genetic patterns related to sex-biased dispersal. This contrasts with studies that have found genetic patterns related to male-biased dispersal on an interpopulation scale. We suggest 3, not exclusive, explanations that may explain these differences: low power to detect sex biases in dispersal tendencies in this panmictic population; a scale-dependent component in dispersal tendencies, where males are overrepresented among interpopulation migrants; and lower reproductive success for dispersing females compared to more philopatric ones.

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APPENDIX I

Wolverines (*Gulo gulo*) used for genetic analysis are listed by catalog number for specimen in the Mammal Collection at the University of Alaska Museum of the North (UAM), Fairbanks (http://www.uaf.edu/museum/af/index.html); latitude and longitude; year (winter) harvested; sex; and age class (NA = voucher specimen not available; * = unknown).

Specimen records (n = 145).—UAM 62905, 67°08′N, 157°87′W, 2000–2001, male, subadult; UAM 62906, 67°08′N, 157°87′W, 2000–2001, female, subadult; UAM 62907, 67°45′N, 159°43′W, 2000–2001, male, subadult; UAM 62908, 67°45′N, 159°43′W, 2000–2001, male, subadult; UAM 62909, *, 1996–1997, male, subadult; UAM 62910, 65°93′N, 161°88′W, 1996–1997, male, subadult; UAM 62911, 66°87′N, 157°15′W, 2000–2001, male, subadult; UAM 62912, 67°57′N, 162°97′W, 2000–2001, female, subadult; UAM 62913, 64°48′N, 162°12′W, 1995–1996, female, subadult; UAM 62914, 64°48′N, 162°12′W, 1995–1996, female, subadult; UAM 62915, *, 1996–1997, female, subadult; UAM 62917, 67°12′N, 160°73′W, 1996–1997, female, subadult; UAM 62918, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62919, 67°23′N, 161°18′W, 1996–1997, female, subadult; UAM 62920, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62921, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62922, 67°23′N, 161°18′W, 1996–1997, female, subadult; UAM 62923, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62924, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62925, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62926, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62927, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62928, 67°23′N, 161°18′W, 1996–1997, male, subadult; UAM 62929, 67°23′N, 161°18′W, 1996–1997, male, adult; UAM 62930, 67°23′N, 161°18′W, 1996–1997, female, adult; UAM 62932, 67°21′N, 159°90′W, 2000–2001, female, subadult; UAM 62933, 67°21′N, 159°90′W, 2000–2001, female, subadult; UAM 62934, 67°35′N, 159°16′W, 2000–2001, female, subadult; UAM 62935, 67°23′N, 161°18′W, 2000–2001, male, subadult; UAM 62936, 67°23′N, 161°18′W, 2000–2001, male, subadult; UAM 62937, 67°23′N, 161°18′W, 2000–2001, male, adult; UAM 62938, 67°23′N, 161°18′W, 2000–2001, male, subadult; UAM 62939, 67°23′N, 161°18′W, 2000–2001, male, adult; UAM 62940, 67°23′N, 161°18′W, 2000–2001, female, subadult; UAM 62941, 67°23′N, 161°18′W, 2000–2001, female, *; UAM 62942, 67°23′N, 161°18′W, 2000–2001, male, *; UAM 62943, 67°23′N, 161°18′W, 2000–2001, male, subadult; UAM 62944, 67°23′N, 161°18′W, 2000–2001, female, subadult; UAM 62945, 67°23′N, 161°18′W, 2000–2001, female, subadult; UAM 62946, 67°23′N, 161°18′W, 2000–2001, male, subadult; UAM 62947, *, 1999–2000, female, subadult; UAM 62948, 66°07′N, 162°70′W, 1998–1999, male, subadult; UAM 62949, 67°57′N, 162°97′W, 1999–2000, female, subadult; UAM 62950, *, 1999–2000, male, subadult; UAM 62951, *, 1999–2000, male, subadult; UAM 62953, *, 1999–2000, male, subadult; UAM 62954, 67°57′N, 162°97′W, 1999–2000, male, subadult; UAM 62955, *, 1996–1997, male, subadult; UAM 62956, *, 1996–1997, male, subadult; UAM 62957, 67°09′N, 160°23′W, 1996–1997, male, subadult; UAM 62958, *, 1996–1997, male, subadult; UAM 62959, *, 1996–1997, male, subadult; UAM 62960, *, 1996–1997, male, subadult; UAM 62961, *, 1996–1997, male, adult; UAM 62963, *, 1996–1997, male, subadult; UAM 62964, *, 1996–1997, male, subadult; UAM 62965, *, 1996–1997, male, adult; UAM 62966, *, 1996–1997, male, subadult; UAM 62967, *, 1996–1997, male, adult; UAM 62968, 65°93′N, 161°88′W, 1996–1997, male, adult; UAM 62969, *, 1996–1997, female, subadult; UAM 62970, *, 1996–1997, female, subadult; UAM 62971, *, 1996–1997, male, subadult; UAM 62972, *, 1996–1997, male, subadult; UAM 62973, *, 1996–1997, female, subadult; UAM 62974, 66°9′N, 162°58′W, 1997–1998, female, subadult; UAM 62975, 66°9′N, 162°58′W, 1997–1998, female, adult; UAM 62976, 66°9′N, 162°58′W, 1997–1998, male, *; UAM 62977, 66°9′N, 162°58′W, 1997–1998, male, subadult; UAM 62978, 65°98′N, 161°13′W, 1998–1999, male, subadult; UAM 62979, 64°48′N, 162°12′W, 1998–1999, male, subadult; UAM 62980, 67°13′N, 162°35′W, 1998–1999, male, subadult; UAM 62982, *, 1998–1999, male, subadult; UAM 62983, 64°48′N, 162°12′W, 1998–1999, female, subadult; UAM 62984, 66°35′N, 154°75′W, 1998–1999, *, subadult; UAM 62985, 66°61′N, 154°32′W, 1998–1999, female, adult; UAM 62986, 67°73′N, 164°54′W, 1998–1999, male, subadult; UAM 62987, *, 1998–1999, male, subadult; UAM 62988, 67°73′N, 164°54′W, 1998–1999, male, subadult; UAM 62989, 67°73′N, 164°54′W, 1998–1999, female, adult; UAM 62990, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 62991, 67°08′N, 157°87′W, 1999–2000, male, *; UAM 62992, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 62993, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 62994, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 62995, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 62996, 67°08′N, 157°87′W, 1999–2000, female, subadult; UAM 62997, 68°14′N, 162°34′W, 1999–2000, female, subadult; UAM 62998, 67°08′N, 157°87′W, 1999–2000, female, adult; UAM 62999, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63000, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63001, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63002, 67°08′N, 157°87′W, 1999–2000, female, subadult; UAM 63003, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63004, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63005, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63006, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63007, 67°08′N, 157°87′W, 1999–2000, male, adult; UAM 63008, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63009, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63010, 67°08′N, 157°87′W, 1999–2000, female, subadult; UAM 63011, 66°07′N, 162°70′W, 1996–1997, male, subadult; UAM 63012, 65°93′N, 161°88′W, 1996–1997, male, subadult; UAM 63013, 67°23′N, 161°18′W, 1997–1998, male, subadult; UAM 63014, 67°23′N, 161°18′W, 1997–1998, male, subadult; UAM 63015, 66°64′N, 155°49′W, 1998–1999, male, adult; UAM 63016, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63017, 67°08′N, 157°87′W, 1999–2000, male, subadult; UAM 63018, 67°45′N, 159°43′W, 2000–2001, female, adult; UAM 63019, 67°45′N, 159°43′W, 2000–2001, male, subadult; UAM 63020, 67°45′N, 159°43′W, 2000–2001, female, subadult; UAM 63815, 67°23′N, 161°18′W, 1996–1997, female, subadult; UAM 63816, 65°93′N, 161°88′W, 1996–1997, male, subadult; UAM 63817, 65°93′N, 161°88′W, 1996–1997, female, adult; UAM 63823, *, 1996–1997, female, subadult; UAM 63825, *, 1996–1997, female, subadult; UAM 63826, *, 1996–1997, female, subadult; UAM 63827, *, 1996–1997, female, subadult; UAM 63828, 67°12′N, 160°73′W, 1996–1997,

female, subadult; UAM 63829, 67°12′N, 160°73′W, 1996–1997, female, subadult; UAM 78225, 67°08′N, 157°87′W, 2001–2002, female, subadult; UAM 78226, 67°08′N, 157°87′W, 2001–2002, male, subadult; UAM 78227, 67°08′N, 157°87′W, 2001–2002, male, adult; UAM 78228, 67°08′N, 157°87′W, 2001–2002, female, subadult; UAM 78229, 67°21′N, 159°90′W, 2001–2002, male, adult; UAM 78231, 67°08′N, 157°87′W, 2001–2002, female, subadult; UAM 78232, 67°08′N, 157°87′W, 2001–2002, male, subadult; UAM 78233, 67°08′N, 157°87′W, 2001–2002, male, adult; UAM 78234, 67°08′N, 157°87′W, 2001–2002, female, adult; UAM 78235, 67°08′N, 157°87′W, 2001–2002, female, adult; UAM 78236, 67°08′N, 157°87′W, 2001–2002, female, subadult; UAM 78237, 67°08′N, 157°87′W, 2001–2002, male, subadult; UAM 78238, 67°21′N, 159°90′W, 2001–2002, male, adult; NA, *, 1996–1997, male, subadult; NA, *, 1996–1997, male, subadult; NA, *, 1996–1997, male, subadult; NA, *, 1996–1997, female, *; NA, 67°23′N, 161°18′W, 1996–1997, male, subadult; NA, 66°12′N, 160°09′W, 1996–1997, male, subadult; NA, 66°92′N, 156°87′W, 1998–1999, male, *; NA, *, 1999–2000, female, *; NA, *, 2002–2003, *, *; NA, *, 2002–2003, *, *; NA, *, 2002–2003, *, *; NA, *, 2002–2003, *, *.