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POPULATION STRUCTURE AND PATERNITY IN AN AMERICAN BLACK BEAR (*URSUS AMERICANUS*) POPULATION USING MICROSATELLITE DNA

Elizabeth A. Sinclair^{1,2}, Hal L. Black¹, and Keith A. Crandall¹

ABSTRACT.—We report genetic microsatellite data from analysis of 71 American black bears (*Ursus americanus*) from the East Tavaputs Plateau in eastern Utah. Heterozygosity was 52.9%, which is lower than other mainland North American populations and possibly reflects low recruitment into the study area. We used a combination of known pedigrees (mother/cubs), relatedness estimates, and paternity estimation using CERVUS to infer single and possible multiple paternity within litters, breeding by pairs over consecutive years, and the possibility of a single male successfully breeding with multiple females in a single year. Estimates of inbreeding effective population size indicate the East Tavaputs Plateau population is part of a larger black bear population.

Key words: black bear, *Ursus americanus*, microsatellites, pedigree, home range, relatedness, paternity, Utah.

Long-term ecological studies of single populations can yield valuable information on the demographics of a species. This information is very powerful, particularly when combined with genetic analyses. Although social structure has been examined in many species, it has generally been restricted to social insects and small mammals (e.g., Crozier et al. 1984, Dallas et al. 1995). Social structure is rarely examined in solitary species such as large mammals, since collection of adequate data is difficult, requiring extended periods of time.

The American black bear (*Ursus americanus*) has a widespread distribution across North America from northern Mexico to Canada and Alaska (Rogers 1999). Habitat loss, hunting, and nutritional deficiencies limit *U. americanus* populations to a portion of their former range (Rogers 1987). Studies of home ranges and dispersal have been carried out using trapping and radio-tracking (e.g., Amstrup and Beecham 1976, Young and Ruff 1982, Horner and Powell 1990). Estimates for home ranges vary greatly among studies (8–1721 km²; summarized in Wooding and Hardisky 1994), which may be influenced by habitat quality (food distribution), climate, topology, and density (Amstrup and Beecham 1976). However, males generally have larger home ranges and move greater distances than females (Rogers 1987, Smith and Pelton 1990).

Few long-term studies have examined the stability of home ranges in *U. americanus*, although Amstrup and Beecham (1976) found well-defined, stable home ranges over 2 consecutive years. If home ranges are relatively stable over time, then we might expect to see large, dominant males forming long-term relationships with particular females and/or fathering litters over consecutive years with those females whose ranges they overlap. Lindzey and Meslow (1977) suggest that in *U. americanus* there are some male-female bonds that last at least 2–3 years. However, both male and female bears are reported as being promiscuous (Rogers 1987). Field observations have noted females mating with several males in both *U. americanus* (Barber and Lindzey 1986, Rogers 1987) and grizzly bears (*U. arctos*; see Craighead et al. 1995). Given these observations, a 2nd prediction is that multiple paternity could occur within litters. Schenk and Kovacs (1995) found evidence for multiple paternity in a Canadian population of *U. americanus*. One male was identified as the father of cubs from 2 litters in a single year. Craighead et al. (1995) found strong evidence for multiple paternity within a litter of *U. arctos* from northwestern Alaska.

In mammals, males show a greater tendency than females for movement from birthplace to initial breeding location (Greenwood 1980).

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Female *U. americanus* are philopatric, with young females making their own home ranges as extensions of their mothers (Garshelis and Pelton 1981, Rogers 1987). Adult male aggression directed toward subadult males may result in their eviction, and hence force dispersal (Bunnell and Tait 1981). Young and Ruff (1982) suggest that this is instigated or controlled by the adult male bears as observed in low cub/yearling/subadult survival, rather than in the number of cubs born. Given this behavior, one would predict a high negative correlation between degree of relatedness among females and geographic distance from natal home range, although Schenk et al. (1998) found no relationship between spatial proximity and average genetic relatedness in their study of a Canadian population of *U. americanus*.

We examined microsatellite DNA variation in a single population of *U. americanus* from the East Tavaputs Plateau of eastern Utah. This population experiences high levels of hunting pressure, with the largest mean number of hunting permits issued and the 2nd largest number of permits filled in the state annually (Blackwell and Evans 1997). Microsatellite DNA loci are highly variable, co-dominant markers, allowing identification of paternal alleles (Craighhead et al. 1995, Keane et al. 1997) and unique multilocus genotypes for individuals (Paetkau and Strobeck 1994, Taberlet et al. 1997). Our objectives were to (1) test for a significant relationship between degree of relatedness and geographic distance from the natal home range in females; (2) assign paternity and hence look for evidence of multiple paternity within litters, males fathering more than 1 litter in a single year, and males fathering cubs with the same female over consecutive years; and (3) estimate the inbreeding effective population size to provide information on the size of this population.

MATERIALS AND METHODS

Study Area

The study area is located on the East Tavaputs Plateau (39°27'N, 109°15'W) approximately 100 km south of Vernal (Fig. 1). It covers approximately 430 km². The topography consists of a series of ridgetops and canyons with elevation ranging from 2190 m to 2520 m. Mean annual precipitation (mostly in the form of snow) is 49 cm. The study area is managed for a variety of uses including natural gas harvest-

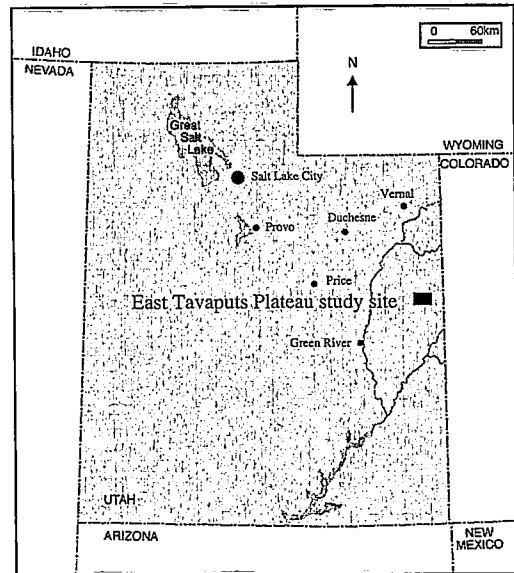


Fig. 1. Location of the East Tavaputs Plateau study site in eastern Utah.

ing, cattle ranching, logging, recreational camping, and sport hunting.

Sampling

Samples were obtained between 1991 and 1999 as part of a long-term population study by H.L. Black (unpublished). The samples include mothers with cubs-of-the-year or yearlings and individuals trapped during the summer. Mothers with radio-collars and their cubs or yearlings were sampled at den sites during winter. During summer, individuals were live-captured using 57-cm barrel traps. All bears except cubs were immobilized with a 2:1 mixture of ketamine hydrochloride and xylazine hydrochloride administered at 6.6 mg · kg⁻¹ body weight intramuscularly with a jab-stick. After immobilization, fresh blood or ear tissue was collected from adults and ear tissue from the cubs. Ear tissue was stored in 100% ethanol and fresh blood was collected in heparinized tubes and frozen. We extracted DNA from these samples using standard phenol/chloroform extraction, precipitated in isopropanol and stored in 50 µL TLE buffer (Sambrook et al. 1989).

Microsatellite Amplification

Microsatellite primers for 7 loci were obtained for *U. americanus* from Paetkau et al.

(1995). These primers were designed for *U. americanus*, but also amplify in other ursids (Craighead et al. 1995, Paetkau et al. 1995, Taberlet et al. 1997). Microsatellite loci were amplified via the polymerase chain reaction (PCR). Reactions contained 2.5 μ L 10X PCR buffer containing $MgCl_2$ (Perkin Elmer), 2.5 μ L 8 mM dNTPs (Perkin Elmer), 1.0 μ L 10 μ M each primer, 1 μ L template DNA, 0.3 μ L *Amplitaq* Gold (Perkin Elmer), and water to 25 μ L. Reactions were carried out in a 9600 Perkin Elmer thermal cycler for an initial 12 minutes denaturation at 95°C, followed by 15 seconds at 94°C, 30 seconds at 49°C–51°C, 45 seconds at 72°C for 40 cycles, and a final extension for 5 minutes at 72°C. Primers were end-labeled with fluorescent dyes (TET, 6-FAM, or HEX). Products were run on an ABI 377 and scored using the program ABI Genotyper version 2.5. The internal size standard Tamra500 was used to calculate allele sizes.

Genetic Analyses

Variation at the 7 microsatellite loci was summarized by allele frequencies and observed and expected heterozygosities. Hardy-Weinberg equilibrium was assessed by Markov chain permutations using the program GENEPOP (Raymond and Rousset 1995). Parentage and relatedness analyses assume that all loci are independent (not linked). Since the loci used in this study have not been mapped onto chromosomes, we tested for genotypic disequilibrium among pairs of loci in GENEPOP. We applied a Bonferroni correction for multiple tests.

To examine the relationship between geographic distance and relatedness among females, we used home range data (H.L. Black unpublished data) and pairwise relatedness values from 16 females. This subset included adults with established home ranges and 2 female offspring that had grown up and established their own home ranges during this study. Females were monitored for 3 to 9 years (mean = 5.8). The number of telemetry locations recorded for each individual varied from 15 to 92 (mean = 47.6). We generated minimum convex polygons to estimate home ranges using all data points (Kie et al. 1994), as there were few locations collected in some years. Spatial means were calculated where X_{mc} , $Y_{mc} = (\sum X_i/N, \sum Y_i/N)$, X_{mc} and Y_{mc} are mean coordinates of the mean center, X_i and Y_i are the

coordinates for each data point, and N is the number of data points. Pairwise distances were measured between these mean coordinates. We compared matrices for pairwise geographic distance versus allele-sharing distances (Bowcock et al. 1994). We chose this method over other more traditional distance measures that are usually used to compare populations and not individual pairwise distances (see Paetkau et al. 1997 for an evaluation of distance measures, e.g., Paetkau et al. 1998). The allele-sharing distance was defined as 1 minus half the average number of shared alleles per locus. Allele-sharing distances were calculated using the individual to individual genetic distance calculator available at <http://www.biology.ualberta.ca/jbrzusto/>. Pairwise allele-sharing distances were plotted against the geographical distance and regression statistics generated in Excel (Microsoft Corporation).

The Windows-based computer program CERVUS was used to derive likelihood ratios for paternity inference (Marshall et al. 1998). A simulation of parentage analysis was run to estimate the resolving power of the 7 loci, based on their allele frequencies, and to estimate the critical values of the log-likelihood statistic delta (Δ). This statistic took into account the number of candidate males, the proportion of males that were sampled, and gaps and errors in the genetic data (Marshall et al. 1998). Data from a total of 10,000 simulations were used to determine significance. The following parameters were set: number of candidate males = 15, proportion of candidate males sampled = 0.25, proportion of loci typed = 0.95, and error rate = 0.001. We estimated the proportion of candidate males based on the total number of males handled during this study ($n = 60$) and complete genotypes for 15 of these males that could be potential fathers; we assumed that not all males were trapped/sampled during our study. The paternity analysis compared genotypes of candidate parents (males) to the offspring genotypes (taking into account the genotype of the known parent: the mother). Candidate males were excluded based on 1 or more allelic mismatches. Males that were 5 years of age or older at the proposed time of conception were considered to be candidate fathers.

Pairwise relatedness estimates were generated using the program Kinship v1.2 (Goodnight and Queller 1999). We assumed parent-

TABLE 1. Allele frequencies and observed and expected heterozygosities for the *U. americanus* population in the East Tavaputs Plateau. Significant deficits ($P < 0.01$) of heterozygotes from H-W expected values indicated by *. Allele names are listed by size in base pairs. Sample sizes are given in parentheses.

Locus	Alleles/Frequencies								He	Ho
G1A (66)	182 0.053	184 0.015	186 0.621	188 0.288	196 0.023				0.532	0.561
G1D (71)	172 0.070	174 0.127	176 0.493	180 0.056	184 0.254				0.673	0.620
G10B (71)	160 0.655	162 0.014	164 0.014	166 0.289	168 0.028				0.490	0.366*
G10C (70)		95 0.007	97 0.514	101 0.479					0.510	0.571
G10L (69)	138 0.261	143 0.188	148 0.152	158 0.007	162 0.333	164 0.015	170 0.036	172 0.007	0.766	0.768
G10M (65)		194 0.146	196 0.269	198 0.539	200 0.008	202 0.039			0.619	0.431*
G10P (60)		169 0.733	171 0.008	173 0.125	175 0.075	179 0.058			0.441	0.383
\bar{x}									0.576	0.529
$s^2_{\bar{x}}$									0.043	0.053

offspring pairs and full siblings were related by 0.5 (as they share half of their genes on average), half siblings by 0.25, and unrelated individuals by 0.0 in a randomly mating population (Hamilton 1964a, 1964b). These values were used to support potential relationships among pairs of individuals when a candidate father was not identified.

Effective population size (N_e) was estimated from heterozygosity (H) and the mutation rate (μ), given that heterozygosity has been estimated for this *U. americanus* population. We used a mutation rate of 2×10^{-3} (Craighead et al. 1995), based on estimates for grizzly bears. At mutation-drift equilibrium, under an infinite allele model (IAM), $H = 4N_e \mu / (1 + 4N_e \mu)$ (Crow and Kimura 1970). For a stepwise mutation model (SMM), $H = 1 - (1 + 8N_e \mu)^{-1/2}$ (Ohta and Kimura 1973). We used both models to obtain a range for our N_e estimate since the true model of mutation for most microsatellite loci is probably somewhere in between (see two-phase model [TPM] of Di Rienzo et al. [1994]).

RESULTS

Seventy-one *U. americanus* individuals, 35 females and 36 males, were genotyped for 7 microsatellite loci. This included 19 males that had reached breeding age (greater than 5 years old) by the end of this study and 33 cubs with

known maternity, of which 1 had reached sexual maturity and produced 3 litters of her own. Eighteen mother/cub groups with litter sizes of between 1 and 4 cubs were genotyped, with 8 of these containing 2 or more cubs. There was a mean of 5.1 alleles per locus and an observed heterozygosity of 52.9% across the sampled population (Table 1). All individuals had unique multilocus genotypes. Five of the 7 loci were in Hardy-Weinberg equilibrium (G1A, G1D, G10C, G10L, and G10P). Significant deficits of heterozygotes were observed at G10B and G10M ($P < 0.01$ after a sequential Bonferroni correction). There was no evidence for genotypic disequilibrium (Table 2), indicating an assumption of independence of loci was valid. On only 1 occasion did the maternal genotype not match with her cub; the mother was 173/173 (locus G10P) and her cub was 169/169. Since tissue samples were collected from cubs at the den sites during winter, this mismatch may be a mutation of at least 1 allele at this locus, rather than an adoption of a cub by this female.

There was no significant relationship between allele-sharing distances and geographic distance for pairwise comparisons among 16 females ($r^2 = 0.0019$, $P = 0.6286$). Mean relatedness across the whole sample was slightly negative, -0.013 ± 0.306 , but close to 0 as expected in a randomly mating population. Mean pairwise relatedness estimates for known full

TABLE 2. Genotype linkage disequilibrium in *U. americanus*. *P* is significant at 0.0024 after a sequential Bonferroni correction.

Locus 1	Locus 2	<i>P</i> -value	$s_{\bar{x}}$
G1A	G1D	0.3542	0.030
G1A	G10B	0.2970	0.025
G1D	G10B	0.8891	0.018
G1A	G10C	0.1169	0.010
G1D	G10C	0.3699	0.019
G10B	G10C	0.3389	0.019
G1A	G10L	0.2920	0.029
G1D	G10L	0.4764	0.037
G10B	G10L	0.2735	0.033
G10C	G10L	0.0046	0.002
G1A	G10M	0.4012	0.028
G1D	G10M	0.4621	0.032
G10B	G10M	0.5072	0.031
G10C	G10M	0.1448	0.010
G10L	G10M	0.3165	0.032
G1A	G10P	0.7286	0.027
G1D	G10P	0.4083	0.028
G10B	G10P	0.278	0.027
G10C	G10P	0.9065	0.008
G10L	G10P	0.0666	0.014
G10M	G10P	0.8058	0.019

siblings and mother/cub sets were also as expected ($n = 17$, 0.453 ± 0.173 and $n = 21$, 0.553 ± 0.212 , respectively). Relatedness among known half siblings was also close to expected ($n = 11$, 0.184 ± 0.283) despite the difficulty in positively identifying this relationship from our data set.

Results from the simulation study (CERVUS) indicated we would obtain poor paternity identification (Table 3). No fathers were identified at the strict level (95%) and only 1 was significant at the 80% confidence level. This provides some support for multiple paternity since this male was not identified as the father of the 2nd cub from the same litter. The relatedness estimate for these cubs was 0.200, close to that expected for half siblings. However, the hypothetical paternal genotype for this litter indicated that a single male could be responsible for the litter (a maximum of 2 alleles per locus were required).

Given that, at most, we have sampled only 1 father of cubs genotyped in this study, we make several observations relating to paternity. These observations are based on the number of paternal alleles required to explain paternity in a litter and relatedness estimates. There were 3 females for which we genotyped 3 litters. In each case, 3 paternal alleles were required to explain the cub genotypes at locus G10L (2 lit-

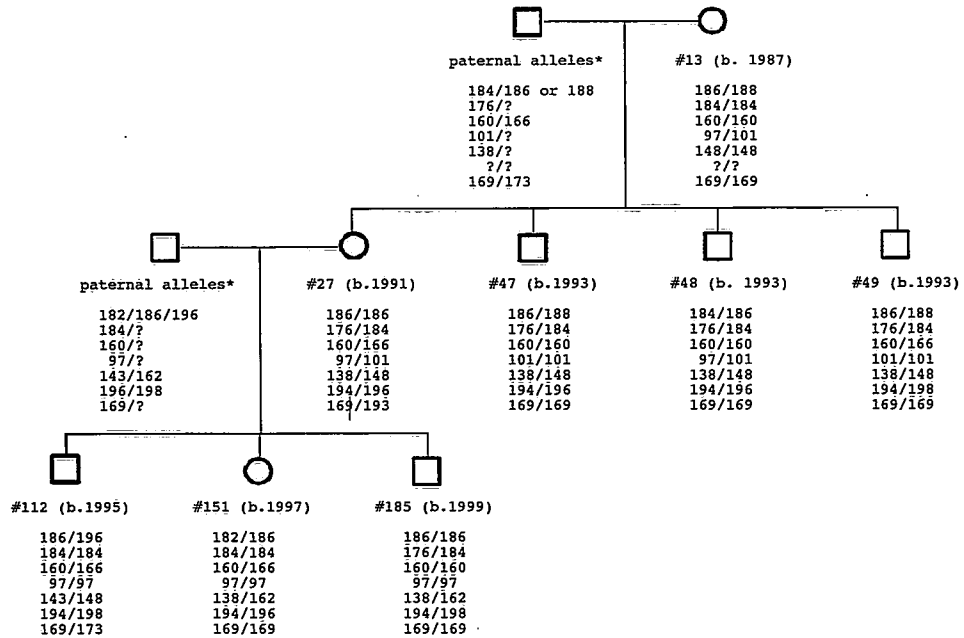
ters), G1D (1 litter), and G1A (1 litter), implying different fathers for litters in different years. There was also evidence for successful matings with the same male over consecutive litters: female #27 (Fig. 2) and cubs #151 (born 1997) and #185 (born 1999) had a relatedness value of 0.518 ($P < 0.05$) and less than 3 alleles were required to explain the hypothetical paternal genotype. Evidence exists for a single, unsampled male fathering litters from 3 different females in 1997. This was based on the paternal genotype requiring only 2 alleles per locus to explain the cub genotypes and their relatedness at the full sibling level (range = 0.499–0.773, $P < 0.05$). These females have either overlapping or geographically close home ranges, so it is possible that the putative father could have successfully mated with all 3 females. We were unable to obtain a complete genotype for a mother of 3 cubs from the same litter. However, it appears likely that more than 1 male fathered these cubs based on their relatedness values (#52 with #53 and #54 = 0.215 and 0.019, respectively, and #53 with #54 = 0.845).

DISCUSSION

Amplification of *U. americanus* DNA using microsatellites has shown that we can uniquely identify individuals (including full siblings) and has shown the inheritance of alleles through known pedigrees. Levels of variation (allelic diversity and heterozygosity) for the East Tavaputs Plateau population are intermediate to those given for other *U. americanus* populations. Estimates for 2 mainland Canadian populations, West Slopes, British Columbia (9.5; 81%), and La Mauricie National Park, Quebec (8.6; 82%), were much higher; an isolated Louisiana population (3.8; 47.4%; Boersen et al. 2003) and the island population on Newfoundland (4.0; 41%) had considerably lower levels of variation (summarized in Paetkau et al. 1997). The lower number of alleles per locus and heterozygosity in the East Tavaputs Plateau, compared to other sampled populations of *U. americanus*, may be indicative of a higher level of inbreeding or mortality. Habitat that provides food resources for black bears is marginal in years of drought and/or when late spring freezes destroy hard and soft mast crops (Tolman 1998). This occurred in the summer of 1995 and again in 2000, resulting

TABLE 3. Critical scores and number of black bear paternity tests predicted to be resolved by simulation using the program CERVUS. Results for relaxed (80%) and strict (95%) confidence are shown, along with the proportion of paternity tests in which a male fulfilled the required criterion.

Simulation (N = 10,000)	Mother sampled		Mother unsampled	
	80%	95%	80%	95%
Critical value of Δ	2.46	4.16	2.90	4.70
Proportion of paternities	15.0%	7.0%	7.0%	1.0%



*It is possible that the same 'unknown father' may be responsible for both the 1991 and 1993 litters of female #13. However, at least two males are responsible for the three litters of #27.

Fig. 2. Pedigree for mother/cubs for female #13. Genotypes are given for loci in the following order: G1A, G1D, G10B, G10C, G10L, G10M, and G10P.

in poor survival of cubs and perhaps yearlings (Tolman personal observation). Cub mortality was high throughout this study, ranging between 43% and 75%, and there was a significant male-biased sex ratio (Tolman 1998). The genetic estimate of effective population size estimated under the IAM was 142 and 222 under the SMM. Given that the relationship between N_e and N is usually close to 0.1 for large mammals and that the total number of animals sampled from this population during our study period is less than 200, we suggest that it is part of a wider, more continuous *U.*

americanus population which extends further north in Utah and east across the Colorado border. We have 2 records of marked bears from the East Tavaputs Plateau being captured in Colorado, moving approximate distances of 70 and 320 km. These observations indicate that animals in our study area are part of a larger and more wide-ranging population, and hence managers need to make and implement decisions for a larger geographic area.

The deviation of 2 loci (G10B and G10M) from Hardy-Weinberg equilibrium may be due to null alleles (Foltz 1986, Callen et al. 1993).

These are usually identified when a population is out of Hardy-Weinberg equilibrium or when genotypes in known pedigrees are incorrect. All except 1 of our pedigrees were correct (see above). An alternative explanation for a deviation from Hardy-Weinberg equilibrium at the 2 loci may be that the assumption of random mating is not being met, or that there is a low level of inbreeding (supported by lower overall heterozygosity).

Home range data from radio-collared females indicated that, although there may be some seasonal shift in home ranges, they have remained stable over the past 9 years. In years of low food supply, several females temporarily left their traditional home ranges to feed on localized mast crops (H.L. Black personal observation). Given that *U. americanus* females are philopatric, we expected the relationship between geographic distance and genetic relatedness to hold true. However, this was not the case. The low number of females used in this comparison ($n = 16$) and limited geographic range over which this analysis was performed may have obscured the true relationship. Our measure of geographic distance did not take into account the topographical features, which may also interfere with this relationship. However, a similar result was also obtained by Schenk et al. (1998), indicating that home range overlap is not restricted to closely related females. The nonsignificant result suggests that factors such as the availability of home ranges (created by the death of an adult female) and food (within the ranges) may have a greater influence in the population structure.

The CERVUS analysis was able to assign paternity in a single case at the relaxed 80% confidence level. Schenk and Kovacs (1995) also had a very low rate of paternity assignment ($n = 36$ males). The lack of paternity assignments in both studies may be due to large, older adult males in the population not having been sampled or having been subsequently removed by hunters or other sources of mortality. The use of larger barrel traps in the future may enable these larger males to be sampled. Many of the males sampled and genotyped during this study were probably too young to have fathered cubs. The only potential father identified in the Schenk and Kovacs (1995) study was 15 years old, while in

our study, the candidate father would have been only 6 years old at the time of conception. All of our 15 candidate males were between 5 and 9 years old in 1999 (the last year we genotyped cubs). In a paternity study of grizzly bears, Craighead et al. (1995) concluded that 49% of breeding-age males greater than 9 years old were successful breeders (and none younger), and multiple paternity was assigned in one-third of known litters with 2 or more cubs. If it is the older males being more reproductively successful, then it is not surprising that we were unable to obtain higher paternity assignment in this study.

Genetic variation can be used to interpret biological patterns at many different levels. Here we examined microgeographic variation in relation to paternity, home ranges, and genetic relatedness among individuals, using heritable markers. The combination of analyses using genetic markers with environmental and behavioral parameters can be a powerful approach, particularly in understanding population structure for wildlife management. In conclusion, we were able to obtain information on the inheritance of microsatellite alleles through examining data over several generations. Given the breeding structure in *U. americanus*, it is expected that multiple paternity does occur. We were able to identify only 1 father. Evidence for multiple paternity from this data set was based on the number of paternal alleles required to explain cub genotypes and relatedness estimates. Further sampling of this population to include older males (maintaining home ranges within the study area) should help in assigning paternity. It will also provide evidence on whether a dominant male, whose home range overlaps several females, usually fathers cubs within his range with more than 1 female in a year and whether he fathers consecutive litters with the same female(s).

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