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Wolverine Confirmation in California after Nearly a Century: Native or Long-Distance Immigrant?

Abstract

We photo-verified the presence of a wolverine (*Gulo gulo*) in California for the first time in 86 years during February 2008. Herein we document the process of determining the origin of this wolverine using genetic, stable carbon ($\delta^{13}C$) and stable nitrogen ($\delta^{15}N$) isotope information. The wolverine's origin was significant because it is a state-threatened species and California represents a historically unique genotype of wolverines in North America. We obtained both photographs and noninvasively-collected genetic evidence (scat and hair). DNA analysis revealed the animal was a male and not a remnant of a historical California population. Comparison with available data revealed the individual was most closely related to populations from the western edge of the Rocky Mountains. This represents the first evidence of connectivity between wolverine populations of the Rocky and Sierra Nevada Mountain Ranges.

Introduction

Wolverines (*Gulo gulo*) once occurred in California, but the last verified specimen was collected in 1922 (Grinnell et al. 1937, Aubry et al. 2007). Trapping and control programs were the most likely cause for the wolverine's decline and extirpation (Dixon 1925, Grinnell et al. 1937, Dunlap 1984). The last known population occurred at very low densities in alpine and sub-alpine (2500-4000 m) habitats in the southern Sierra (Grinnell et al. 1937). Since 1922 there have been numerous unverified reports of wolverines in the state (Ruth 1954, Jones 1955, Cunningham 1959, Yokum 1973, Schempf and White 1977, Kovach 1981), but anecdotal evidence is fraught with potential errors of interpretation (McKelvey et al. 2008). However, recent surveys using detection devices that can produce verifiable evidence, suggest that the former wolverine population has been extirpated from California (Kucera and Barrett 1993, Hudgens and Garcelon 2007, Schwartz et al. 2007).

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Figure 1. Initial photograph of the wolverine (*Gulo gulo*) in California taken from a digital remote camera station on 28 February 2008 at 0805 Pacific Standard Time (PST). The camera was set to document the occurrence of American marten (*Martes americana*).

Surprisingly, during a study of the American marten (*Martes americana*) near Truckee, California, we photographed a wolverine at a remotely triggered camera station (Figure 1). Wolverines are classified as state threatened and were a candidate for listing as a federally endangered species (CDFG 2008, USFWS 2008). The animal was assumed to be either a survivor from a native California population, a natural disperser, or a captive animal that was accidentally or deliberately released. If the animal was a remnant of the last known wolverine population in California, it was much further north than expected. If the wolverine naturally dispersed, we assumed that it would have originated from one of the 2 closest known populations: the Rocky Mountains of Idaho or Montana (~ 650 km) or the Cascades of northern Washington (~1000 km) (Aubry et al. 2007). If the animal was accidentally or deliberately transplanted, we presume it could have come from any population including those in Alaska or Canada. Lastly, determining the sex of the animal was important as a female might imply a nearby population or, more so than a male, support the origin as accidental or deliberate release.

Our initial strategy was to explore the possibility that the animal may be a remnant of a native population. Schwartz et al. (2007) sequenced genetic samples from 7 of the 9 known California wolverine museum specimens, and determined that they were genetically unique from other North American wolverines. Genetics for many of the North American wolverine populations have been characterized (Kyle and Strobeck 2001, Cegelski et al. 2006, Schwartz et al. 2007) such that this individual could be assigned to a contemporary or historical population. However, we first needed to collect a DNA sample. Herein we describe the methods used to search for and analyze DNA samples from this wolverine and how genetic methods coupled with stable isotope analyses, as well as reference samples obtained from archived museum specimens, were used to address the question of this wolverine's origin.

Methods

The first wolverine photograph occurred within an array of 30 cameras and 77 bait stations operational from 10 January–23 March, 2008 (Figure 2).

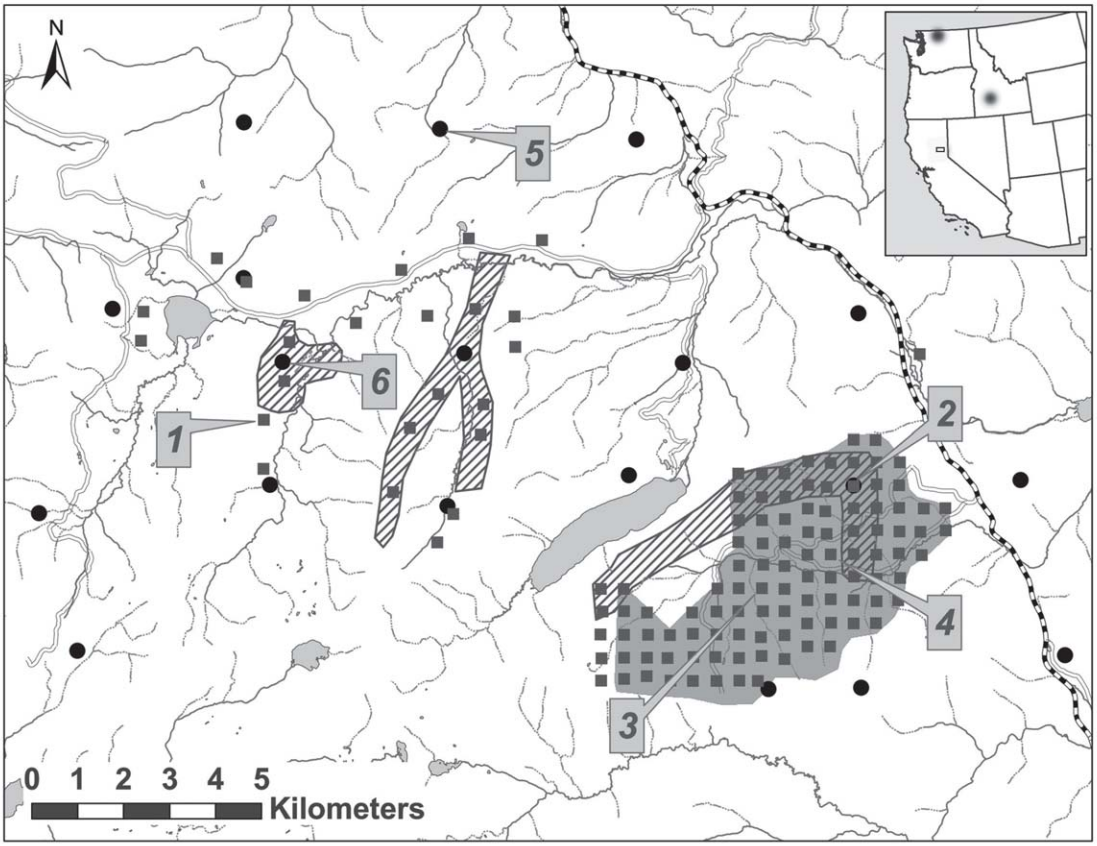

Figure 2. The array of stations used to detect the wolverine found in California. The original grid used to detect American marten (squares) was in operation from 10 January-23 March, 2008. An additional regional grid with alternating hair snare and carcass stations was established following the detection (circles) and was in operation from 09 March – 24 April, 2008. Areas were covered by the scat dog teams from 10–13 March 2008 (hatched) and by human observers (grey) from 02-23 March 2008 in search for genetic material. Results from 2008 surveys are as follows: 1) Large unconfirmed tracks photographed 19 February, later identified to have a mustelid gait by M. Elbroch; 2) the location of the first photograph taken 28 February; 3) the second series of photographs from 13 March; 4) tracks followed 14 March for over 5 linear km from the station with 13 March photographs; 5) a 14- photograph series taken 16 March and the site where all 6 genetic samples were collected; 6) a single photograph taken 0302 PST on 19 March. A location map shows the approximate position and the closest wolverine populations in the Cascades, WA, and the Sawtooth Range, ID. Map created by the Tahoe National Forest GIS Department.

Immediately after the original wolverine photograph we expanded efforts to re-photograph the animal and collect DNA for genetic analysis. This included establishing a 16-station grid with stations placed approximately 5 km apart over an area of 150 km^2. Detection methods alternated between barbed-wire hair snares (Mulders et al. 2007, Kendall and McKelvey 2008) and carcass stations where portions of deer (*Odocoileus hemionus*) were used as bait, all stations were monitored by remote-sensor cameras (Kays and Slauson 2008). Dogs trained to detect wolverine feces (Wasser et al. 2004, MacKay et al. 2008) searched over 100 linear km. Two teams, each consisting of a dog, its handler, and an orienteer, followed transects in areas near the initial photograph and along nearby ridgelines (Figure 2). Observers also searched a 35 km^2 area for fecal, urine, and hair samples (Hedmark 2004, Ulizio et al. 2006). Researchers and volunteers snowshoed or skied along transects such that there were two to four people, each 5 m apart, looking for tracks, scat, urine, and sign (Figure 2). This effort began within a week of the first wolverine photograph. All scat and hair samples found were collected, stored, and documented with corresponding spatial

information. We sent all samples to the Wildlife Genetics Laboratory (U.S. Forest Service, Missoula, MT) accompanied by a forensic chain of custody form (Budowle et al. 2005).

We processed the samples in a laboratory dedicated to the extraction of DNA from noninvasive samples following forensic and security protocols. Mitochondrial DNA (mtDNA) was amplified using universal mammalian primers (Shields and Kocher 1991) to identify species. Wolverine samples were subsequently sequenced at a 344 bp region of the left domain of the mtDNA control region (Wilson et al. 2000, Schwartz et al. 2007). This region of the genome has been previously examined to assess wolverine haplotype diversity (Wilson et al. 2000, Walker et al. 2001, Tomasik and Cook 2005, Cegelski et al. 2006, Schwartz et al. 2007) resulting in detection of 17 wolverine haplotypes, including two from historical California samples (Schwartz et al. 2007).

Wolverine samples were further examined at 16 microsatellite loci to assess the geographic origin of the sample. Nine of the loci were described by Schwartz et al. (2007), and these were supplemented with *Ggu216* (Duffy et al. 1998), *Mvis72, Mvis075* (Flemming et al. 1999), *Lut604* (Dallas and Piertney 1998), *Ma9*, *Gg3*, and *Tt1* (Davis and Strobeck 1998). We used an SRX/SRY analysis to determine sex (Hedmark et al. 2004).

We used program STRUCTURE (Pritchard et al. 2000) to group 261 genetic samples (Schwartz et al. *In press*) from Yellowstone, Wyoming, Washington, Sawtooth Mountains (Idaho), western and central Montana, Alaska, Ontario, historical California samples, a captive population with founders from the Yukon Territory, and the unknown sample from the California wolverine. No samples were available from Alberta or Oregon's historical specimens (Table 1). STRUCTURE assumes that collected samples represent K populations and uses a Markov Chain Monte Carlo (MCMC) method to assign individual multi-locus genotypes to populations, minimizing Hardy-Weinberg deviations and linkage disequilibrium. For this analysis we also provided *a priori* location and grouping data to the program by assigning each

TABLE 1. Frequency of haplotype A in wolverines (*Gulo gulo*) from known sampled populations.

Location	Frequency of Haplotype A	References
Sawtooth Mountains, Idaho (n = 13)	100%	Schwartz et al. 2007
Greater Montana (n = 60)	97%	Schwartz et al. 2007
Rocky Mountain Front, Montana (n = 44)	91%	Cegelski et al. 2006
Gallatin, Montana (n = 25)	80%	Cegelski et al. 2006
Known captive (n = 12)	66%	Copeland, unpubl. data
Williston Lake, British Columbia (n = 37)	58%	Cegelski et al. 2006
Northwest Territories[1] (n = 15)	45%	Tomasik and Cook 2005
Northwest Alaska[1] (n = 22)	30%	Tomasik and Cook 2005
Southeast Alaska[1] (n = 12)	30%	Tomasik and Cook 2005
Grande Cache, Alberta (n = 17)	29%	Cegelski et al. 2006
Southern Alaska[1] (n = 17)	25%	Tomasik and Cook 2005
Crazy and Little Belt Mountains (n = 19)	21%	Cegelski et al. 2006
NT Canada (n = 41)	20%	Wilson et al. 2000
Nunavut[1] (n = 47)	5%	Tomasik and Cook 2005
California (n = 7)	0%	Schwartz et al. 2007
Kenai, Alaska (n = 22)	0%	Tomasik and Cook 2005
Mongolia (n = 5)	0%	Schwartz et al. 2007
Northern Alaska (n = 10)	0%	Tomasik and Cook 2005
Scandinavia (n = 169)	0%	Walker et al. 2001
Washington (n = 5)	0%	Aubry and Schwartz, unpubl. data

[1]Note: data from Tomasik and Cook (2005) estimated from pie charts in their Figure 1.

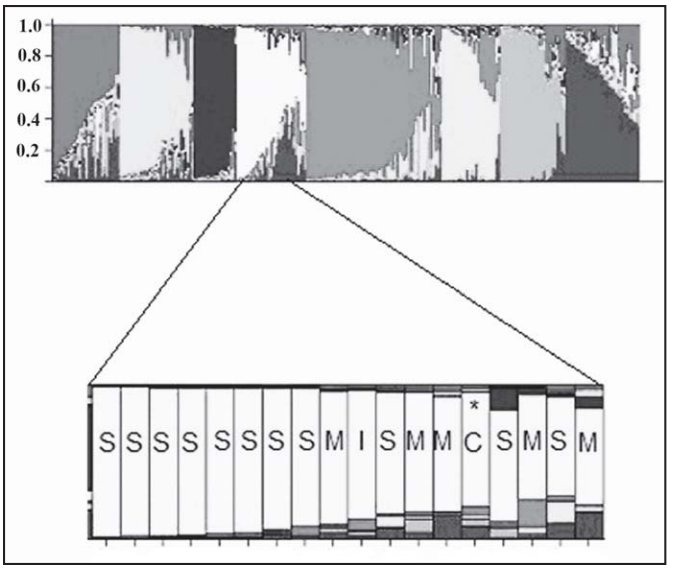

Figure 3. Estimated population structure from STRUCTURE analyses for 8 population groups (K). Each individual is represented by a thin horizontal line divided into 8 population (K) segments that represent the individual's estimated membership fractions (q) in each of the clusters. The bottom part of the figure highlights the "cluster" which is composed of samples from the Sawtooth Mountains (S), samples from northwest and north of the Sawtooth Mountains (I), state harvested samples in Montana (M), and the California wolverine documented in this study (C).

of the samples to one of 16 different groups based on either sampling effort (i.e., field study) or geographic location. Subsequently we examined where the California wolverine sample was assigned using STRUCTURE's admixture model with a "burn-in" of 10,000 and 100,000 MCMC repetitions. Because different runs can produce different likelihood values (Evanno et al. 2005), we conducted 10 independent runs in order to quantify the variation in log-likelihood for each K (Figure 3). The number of inferred groups was evaluated (between 1 and 10). The most supported K maximized LnP(D), the log-likelihood of the data at each step of the MCMC minus half the variance. While the number of inferred groups can be sensitive to isolation by distance effects, we only used STRUCURE to evaluate the proportion of membership of the California sample (Schwartz and McKelvey 2008).

Hair samples from ten wolverine specimens were analyzed for their stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope composition. These samples were from the historical California wolverine population (n = 5), southeast Alaska, northwest Canada, Idaho, Montana (n = 1 from each location), and from the unknown California wolverine (n = 2). Each hair sample was cleaned with distilled water, air-dried to a constant weight, and cut into 0.5 to 1.5 mm pieces. Two mg of each hair sample was weighed and placed into a 3 x 5 mm tin capsule, sealed and then combusted with an elemental analyzer (ANCA-SL, PDZ Europa Scientific) connected to a continuous flow isotope ratio mass spectrometer (model 20-20, PDZ Europa Scientific) housed in the Center for Stable Isotope Biogeochemistry at U.C. Berkeley. Stable isotope data are expressed in delta (δ) notation (deviations from the standard) with units of parts per thousand, given the symbol, ‰ (Dawson and Brooks 2001). Long-term external precision for the $\delta^{13}C$ and $\delta^{15}N$ analyses are ± 0.22‰ and 0.25‰, respectively. With respect to meaningful differences it is generally agreed that for $\delta^{13}C$ a 1.0 to 1.5‰ difference among groups is significant (Hobson 1999, Hobson and Wassenaar 2001) and that very positive $\delta^{15}N$ values indicates that animals feed higher on the food chain (Hobson 1999).

Results

The first wolverine photograph was taken on 28 February 2008. Seventeen additional photographs were obtained at 3 different locations on 13, 16, and 19 March 2008 within 3.2, 11.8, and 12.8 km of the original location (Figure 2). We collected a total of 82 fecal or hair samples from all field efforts (Figure 2). Two fecal and four hair samples collected from the one photographic bait station were determined to be from a wolverine (Figure 2). Samples were all found within 10 m of the detection station. All six of these samples were haplotype A, a result that was independently verified by the USGS Alaska Science Center's genetics laboratory. Haplotype A has not been reported in Washington or California, yet is the dominant haplotype in the U.S. Rocky Mountains (Table 1).

The microsatellite and gender analyses determined that all 6 samples were from the same

male with a match probability of 6.297 x 10^{-11} (meaning the probability of two random wolverines matching at the microsatellites analyzed by chance alone was greater than 1 in 15.8 billion). STRUCTURE revealed that the most supported number of population groupings among the 261 microsatellite samples from the various North American populations was 8. This analysis placed the contemporary California wolverine into a group primarily comprised of individuals from the Sawtooth Mountains of Idaho with a confidence level of 73.4% (Figure 3). The second highest group membership was with samples largely from Montana (8.9%). Comparatively, animals captured in the Sawtooth Mountains had an average self membership of 88.0% (SD 11.2, range 64.6–97.1). Thus, the microsatellite data indicate that the California wolverine assigns to the Idaho population with only slightly lower confidence than individuals known to be from the Idaho population. Examining STRUCTURE simulations with K = 7-9 produced nearly identical results, suggesting our data were relatively insensitive to the number of groups identified.

The carbon and nitrogen isotope analyses supported our genetic results. The carbon isotope composition of hair revealed that the unknown California wolverine (average -27.3‰) was more closely allied to Rocky Mountain individuals (average -28.5‰) than the southern Alaska/northwest Canada samples (average -25.2‰), or the historical California samples (average -23.7‰, Figure 4). The nitrogen stable isotope data reveals that the historic California animals were eating across different trophic levels (range 7.6–9.4‰), the Rocky Mountain animals' diets were strictly carnivorous (range 9.5–9.9‰), and the unknown California wolverine fell in between at 8.2‰. The carbon and nitrogen stable isotope data in combination suggest that within the unknown individual's lifetime it foraged in the Rocky mountain region before immigrating into California.

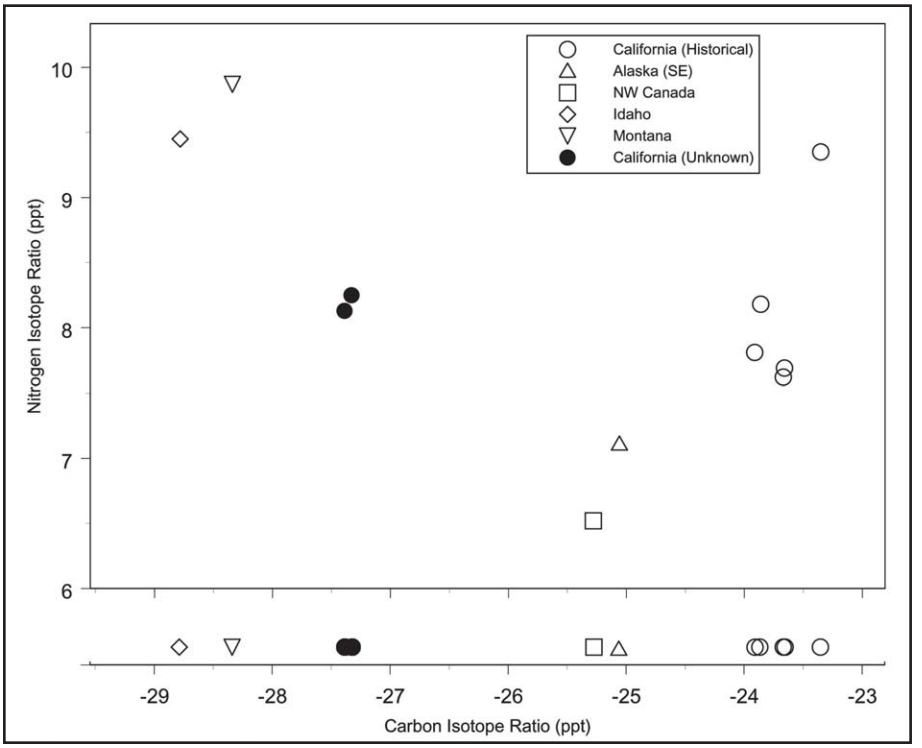

Figure 4. The stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope composition, in parts per thousand (ppt), of hair analyzed from known specimens and 2 unknown samples from the California wolverine. Sample results from $\delta^{13}C$ axis were simplified below to exemplify the distance (ppt) between locations.

Discussion

Mitochondrial and microsatellite genetic evidence, as well as our stable isotope analyses, suggests that the male wolverine we detected in California was most closely related to populations in the western Rocky Mountain region. The ability of wolverines to make long distance movements suggest that they can re-colonize former ranges given enough time (Vangen et al. 2001, Flagstad et al. 2004). In Norway, some populations were considered functionally extinct in the 1960s but have since recovered via natural recolonization (Flagstad et al. 2004). This was accomplished by females and males traveling distances exceeding 100 and 500 km, respectively. Wolverines typically disperse around 13 months of age (Vangen et al. 2001, Inman et al. 2007). Dispersal has been known to occur between January and May (Magoun 1985) and new research in the Rocky Mountains suggests dispersal can occur during multiple years in pulses between February and April (Robert M. Inman, Wildlife Conservation Society, personal communication). Thus, the timing of the detections in California is consistent with the time of year when dispersal movements are expected.

Wolverines have been documented crossing a number of significant natural and artificial discontinuities in the landscape (Inman et al. 2004). Roads are a serious concern as a barrier for wildlife, especially for carnivores that have extensive home ranges (Austin 1998, Forman and Alexander 1998, Packila et al. 2007). Roads are unlikely to be a complete barrier to wolverine movement, but depending on the amount of traffic and location, may affect wolverine behavior. During a long-term wolverine study in the Greater Yellowstone region, researchers documented a total of 43 crossings of U.S. and state highways by 12 wolverines (Packila et al. 2007). Although the route the wolverine may have used to arrive in California is unknown, it would have had to cross numerous barriers.

There are some caveats to our analysis that need to be acknowledged. First, using STRUCTURE, or any clustering algorithm, to discern the number of biologically meaningful groups is difficult for a species as highly vagile as the wolverine and any species that is primarily structured by geographic distance. In fact Schwartz and McKelvey (2008) show that clustering programs often fail to detect the proper number of population groups (K) when the sampled individuals exhibit genetic isolation due to distance. Schwartz et al. (*In Press*) also show that wolverines are structured primarily by ecological distance, although a large component of ecological distance is geographic distance. However, using *a priori* groups and classic assignment tests also produced the same results as the STRUCTURE analysis (data not shown).

With regards to our stable isotope analyses, it is important to acknowledge that our interpretation is based on a very small number of reference samples with known origins. Ideally, multiple samples for each location and from a diversity of populations would have been used. This said, the analysis of the $\delta^{13}C$ and $\delta^{15}N$ in hair can successfully document both migration patterns and diet (Cerling et al. 2006) and the values we obtained were consistent with modeled isotope values (Bowen and West 2008) where enrichment of $\delta^{13}C$ and depletion of $\delta^{15}N$ levels would be expected during immigration from the Rocky Mountains to California. Without additional samples, our confidence level cannot be quantified and warrants further investigation.

Although the California individual closely matched populations in the Sawtooth Mountain Range, the contemporary genetic signature may differ from available samples collected in the early 1990s (Copeland et al., unpublished data). Other geographic areas also need to be considered before an accurate assessment can be made. There are many areas around the Sawtooths in both Idaho and Eastern Washington where wolverines probably occur but have not been sampled (i.e., the Wallowa Mountains in northeastern Oregon). Genetic analyses have been completed for historical Oregon specimens. Thus, concluding that the individual came from the Sawtooth Mountains would be overstepping the data. Instead, the genetic analysis supports an origin at the western edge of the Rocky Mountain region.

Lastly, we cannot discount that the individual was accidentally or deliberately released. Given the lack of known captive facilities that used Idaho wolverines as source material, and the fact that the last open trapping season in Idaho was in the 1960s (Don P. Kemner, Idaho Department of Fish and Game, personal communication), we think that human–caused movement is unlikely.

The conclusion that the California wolverine traveled from the Rocky Mountains is consid-

ered a unique event that we are fortunate to have documented. Previous analysis, based on small sample sizes, suggests that wolverines in the Rocky Mountains and the Sierra Nevada had no historical connectivity (Aubry et al. 2007, Schwartz et al. 2007). This current observation provides hope that dispersal to, and even recolonization of, long-vacant portions of a species' range is possible.

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Literature Cited

Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. Journal of Wildlife Management 71:2147-2158.

Austin, M. 1998. Wolverine winter travel routes and response to transportation corridors in Kicking Horse Pass between Yoho and Banff National Parks. M.S. Thesis. University of Calgary, Calgary, Alberta.

Bowen, G. J., and J. B. West. 2008. Isotope landscapes for terrestrial migration research. *In* K. A. Hobson and L. I. Wassenaar (editors), Tracking animal migration with stable isotopes. Elsevier, Burlington, MA. Pp. 78-105.

Budowle, B., P. Garofano, A. Hellman, M. Ketchum, Kanthaswamy, W. Parson, W. van Haeringen, S. Fain, and T. Broad. 2005. Recommendations for animal DNA forensic and identity testing. International Journal of Legal Medicine 119:295-302.

CDFG. 2008. State and federally listed endangered and threatened animals of California. Unpublished Report on file at California Department of Fish and Game, Sacramento, CA.

Cegelski, C. C., L. P. Waits, N. J. Anderson, Ø. Flagstad, C. Strobeck, and C. J. Kyle. 2006. Genetic diversity and population structure of wolverine (*Gulo gulo*) populations at the southern edge of their distribution in North America with implications for genetic viability. Conservation Genetics 7:197-211.

Cerling, T. E., G. Wittemeyer, H. B. Rasmussen, F. Vollrath, C. E. Cerling, T. J. Robinson, and I. Douglas-Hamilton. 2006. Stable isotopes in elephant hair document migration patterns and diet changes. Proceedings of the National Academy of Sciences 103:371-373.

Cunningham, J. D. 1959. Wolverine and fisher in the Yosemite region. Journal of Mammalogy 40:614-615.

Dallas, J. F., and S. B. Piertney. 1998. Microsatellite primers for the Eurasian otter. Molecular Ecology 7:1248-1251.

Davis, C. S., and C. Strobeck. 1998. Isolation, variability, and cross-species amplification of polymorphic microsatellite loci in the family Mustelidae. Molecular Ecology 7:1771-1788.

Dawson, T. E., and P. D. Brooks. 2001. Fundamentals of stable isotope chemistry and measurement. *In* M. Unkovich, A. McNeill, J. Pate and J. Gibbs (editors), The Application of Stable Isotope Techniques to Study Biological Processes and the Functioning of Ecosystems. Kluwer Academic Publishers, Dordrecht Pp. 1-18.

Dixon, J. S. 1925. Closed season needed for fisher, marten, and wolverine in California. California Department of Fish and Game 11:23-25.

Duffy, A., A. Landa, M. O'Connell, C. Stratton, and J. Wright. 1998. Four polymorphic microsatellites in wolverine, *Gulo gulo*. Animal Genetics 29:63-72.

Dunlap, T. R. 1984. Values for varmints: predator control and environmental ideas, 1920-1939. Pacific Historical Review 53:141-161.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611-2620.

Flagstad, Ø., E. Hedmark, A. Landa, H. Broseth, J. Persson, R. Anderson, P. Segerström, and H. Ellegren. 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. Conservation Biology 18:667-675.

Flemming, M. A., E. A. Ostrander, and J. A. Cooks. 1999. Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). Molecular Ecology 8:1352-1354.

Forman, R. T., and L. E. Alexander. 1998. Roads and Their Major Ecological Effects. Annual Reviews—Ecological Evolution Systematics 29:207.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-Bearing Mammals of California, University of California Press, Berkeley.

Hedmark, E., Ø. Flagstad, P. Segerström, J. Persson, A. Landa, and H. Ellegren. 2004. DNA-based individual and sex identification from wolverine (*Gulo gulo*) faeces and urine. Conservation Genetics 5:405-410.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326.

Hobson, K. A., and L. I. Wassenaar. 2001. A stable isotope approach to delineating population structure

in migratory wildlife in North America: an example using the loggerhead shrike. Ecological Applications 11:1545–1553.

Hudgens, B. R., and D. K. Garcelon. 2007. Winter carnivore survey finds that wolverines (*Gulo gulo*) are likely extirpated from Sequoia-Kings Canyon National Parks. Unpublished Report on file at Institute for Wildlife Studies, Arcata, CA.

Inman, R. M., K. H. Inman, A. J. McCue, M. L. Packila, G. C. White, and B. C. Aber. 2007. Wolverine space use in Greater Yellowstone. Unpublished Report on file at Wildlife Conservation Society, North America Program, Bozeman, MT.

Inman, R. M., R. R. Wigglesworth, K. H. Inman, M. K. Schwartz, B. L. Brock, and J. D. Rieck. 2004. Wolverine makes extensive movements in the Greater Yellowstone Ecosystem. Northwest Science 78:261-266.

Jones, F. L. 1955. Records of southern wolverine, *Gulo luscus luteus*, in California. Journal of Mammalogy 36:569.

Kays, R. W., and K. M. Slauson. 2008. Remote cameras. *In* R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray (editors), Noninvasive Survey Methods for Carnivores, Island Press, Washington D.C., Pp. 110-140.

Kendall, K. C., and K. S. McKelvey. 2008. Hair collection. *In* R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray (editors), Noninvasive Survey Methods for Carnivores, Island Press, Washington D.C., Pp. 135-176.

Kovach, S. D. 1981. Wolverine, *Gulo gulo*, records for the White Mountains, California. California Fish and Game 67:132-133.

Kucera, T. E., and R. H. Barrett. 1993. The California cooperative wolverine survey: a progress report. Transactions of the Western Section of the Wildlife Society 29:49-53.

Kyle, C. J., and C. Strobeck. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. Molecular Ecology 10:337-347.

MacKay, P., D. A. Smith, R. A. Long, and M. Parker. 2008. Scat detection dogs. *In* R. A. Long, P. MacKay, W. J. Zielinski and J. C. Ray (editors), Noninvasive Survey Methods for Carnivores, Island Press, Washington D.C., Pp. 183-222.

Magoun, A. J. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. Ph. D. Dissertation, University of Alaska. Fairbanks.

McKelvey, K. S., K. B. Aubry, and M. K. Schwartz. 2008. Using anecdotal occurrence data for rare or elusive species: the illusion of reality and call for evidentiary standards. BioScience 58:549-555.

Mulders, R., J. Boulanger, and D. Paetkau. 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark-recapture methods. Wildlife Biology 13:38-51.

Packila, M. L., R. M. Inman, K. H. Inman, and A. J. McCue. 2007. Wolverine road crossings in western Greater Yellowstone Unpublished Report on file at Wildlife Conservation Society, North America Program, Bozeman, MT.

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Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945-959.

Ruth, P. F. 1954. Wolverine seen in Squaw Valley, California. Journal of Mammalogy 35:594-595.

Schempf, P. F., and M. White. 1977. Status of six furbearer populations in the mountains of northern California. Unpublished Report on file at USDA Forest Service and Museum of Vertebrate Zoology, University of California, Berkeley, CA.

Schwartz, M. K., K. B. Aubry, K. S. McKelvey, K. L. Pilgrim, J. P. Copeland, J. R. Squires, R. M. Inman, S. M. Wisely, and L. F. Ruggiero. 2007. Inferring geographic isolation of wolverines in California. Journal of Wildlife Management 71:2170-2179.

Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. *In press*. Wolverine gene flow across a narrow climatic niche. Ecology.

Schwartz, M. K., and K. S. McKelvey. 2008. Why sampling scheme matters: the effect of sampling scheme on landscape genetic results. Conservation Genetetics DOI 10.1007/s10592-008-9622-1.

Shields, G., and T. D. Kocher. 1991. Phylogenetic relationships of North American ursids based on analysis of mitochondrial DNA. Evolution 45:218-221.

Tomasik, E., and J. A. Cook. 2005. Mitochondrial phylogeography and conservation genetics of wolverine (*Gulo gulo*) of northwestern North America. Journal of Mammalogy 86:386-396.

Ulizio, T. J., J. R. Squires, D. H. Pletscher, J. J. Claar, and L. F. Ruggiero. 2006. The efficacy of obtaining genetic-based identifications from putative wolverine snow tracks. Wildlife Society Bulletin 34:1326-1332.

USFWS. 2008. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the North American wolverine as endangered or threatened. Federal Register 73:12929-12941.

Vangen, K. M., J. Persson, A. Landa, R. Anderson, and P. Segerstom. 2001. Characteristics of dispersal in wolverines. Canadian Journal of Zoology 79:1641-1649.

Walker, C. W., C. Vila, A. Landa, M. Linden, and H. Ellengren. 2001. Genetic variation and population structure in Scandinavian wolverine (*Gulo gulo*) populations. Molecular Ecology 10:53-63.

Wasser, S. K., B. Davenport, E. R. Ramage, K. E. Hunt, M. Parker, C. Clarke, and G. Stenhouse. 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. Canadian Journal of Zoology 82:475-492.

Wilson, G. M., R. A. Van Den Bussche, P. K. Kennedy, A. Gunn, and K. Poole. 2000. Genetic variability of wolverines (*Gulo gulo*) from the Northwest Territories, Canada: conservation implications. Journal of Mammalogy 81:186-196.

Yokum, C. F. 1973. Wolverine records in the Pacific Coastal States and new records for northern California. California Department of Fish and Game 59:207-209.