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Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the Western United States

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ABSTRACT

Wildlife populations are often influenced by multiple political jurisdictions. This is particularly true for wide-ranging, low-density carnivores whose populations have often contracted and remain threatened, heightening the need for geographically coordinated priorities at the landscape scale. Yet even as modern policies facilitate species recoveries, gaps in knowledge of historical distributions, population capacities, and potential for genetic exchange inhibit development of population-level conservation priorities. Wolverines are an 8–18 kg terrestrial weasel (Mustelidae) that naturally exist at low densities (~5/1000 km^2) in cold, often snow-covered areas. Wolverines were extirpated, or nearly so, from the contiguous United States by 1930. We used a resource selection function to (1) predict habitat suitable for survival, reproduction and dispersal of wolverines across the western US, (2) make a rough estimate of population capacity, and (3) develop conservation priorities at the metapopulation scale. Primary wolverine habitat (survival) existed in island-like fashion across the western US, and we estimated capacity to be 644 wolverines (95% CI = 506–1881). We estimated current population size to be approximately half of capacity. Areas we predicted suitable for male dispersal linked all patches, but some potential core areas appear to be relatively isolated for females. Reintroduction of wolverines to the Southern Rockies and Sierra-Nevadas has the potential to increase population size by >50% and these regions may be robust to climate change. The Central Linkage Region is an area of great importance for metapopulation function, thus warranting collaborative strategies for maintaining high survival rates, high reproductive rates, and dispersal capabilities. Our analysis can help identify dispersal corridors, release locations for reintroductions, and monitoring targets. The process we used can serve as an example for developing collaborative, landscape-scale, conservation priorities for data-sparse metapopulations.

1. Introduction

As human populations expanded across the globe, many wildlife species, especially carnivores, experienced significant range loss (Fanshawe et al., 1991; Kang et al., 2010; Paquet and Carbyn, 2003). More recently, attitudes and policies have shifted to facilitate species conservation so that expansions into historical range are possible, often through reintroductions (e.g., Bangs et al., 1998; Clark et al., 2002; Raesly, 2001). Reintroductions have the

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potential to improve viability of endangered species (Hebblewhite et al., 2011) and provide many other ecological benefits (Beyer et al., 2007; Dickman et al., 2009). However, in the case of wide-ranging, low-density carnivores whose populations are often threatened, they and the areas where they can exist are often managed by multiple political jurisdictions whose authorities and objectives can differ. In these situations, great gains in conservation success and financial efficiency could be made by developing geographically coordinated priorities at the scale of a viable population (Slotow and Hunter, 2009). Unfortunately, timing of range loss often occurred prior to establishment of accurate definitions of species distribution, and information on potential population numbers is simply unknown. As a result, gaps in knowledge of suitable habitat, population capacities, and potential for genetic exchange across a metapopulation can inhibit development of the most effective landscape-level priorities for aiding species recovery. The need to address these landscape-scale issues is becoming more pressing as climate change threatens to increase fragmentation of many populations (Opdam and Wascher, 2004).

The wolverine (*Gulo gulo*) is a large, terrestrial weasel (Mustelidae) weighing 8–18 kg that has an Holarctic distribution. This facultative scavenger occupies a cold, low-productivity niche (Copeland et al., 2010; Inman et al., 2012a,b) that results in sparse population densities ($\sim$5/1000 km^2) and low reproductive rates (0.7 young/female > 3 yrs/yr) across its range (Golden et al., 2007; Inman et al., 2012a; Lofroth and Krebs, 2007; Persson et al., 2006). As a result, wolverine populations are relatively vulnerable due to their small size and limited capacity for growth (Brøseth et al., 2010; Persson et al., 2009). Wolverines were extirpated, or nearly so, from their historical distribution within the contiguous US by about 1930 and unregulated human-caused mortality was likely responsible (Aubry et al., 2007). Wolverines have recovered to a considerable degree (Anderson and Aune, 2008; Aubry et al., 2007; Aubry et al., 2010; Copeland, 1996; Inman et al., 2012a), however the species will face a new set of habitat-related challenges in the 21st Century such as rural sprawl, roads, recreation, and climate change (Gude et al., 2007; Krebs et al., 2007; McKelvey et al., 2011; Packila et al., 2007). Wolverines were recently designated a candidate for listing in the contiguous US under the US Endangered Species Act (US Fish and Wildlife Service, 2010; US Fish and Wildlife Service, 2013).

Wolverine habitat in the contiguous US appears to consist of disjunct patches of mountainous, high alpine areas inhabited at low densities and requiring dispersal across intervening areas (Copeland et al., 2010; Inman et al., 2012a), likely a prime example of a metapopulation (Hanski and Gaggiotti, 2004). The metapopulation concept has evolved from island biogeographic theory (MacArthur and Wilson, 1967) into complex estimates of population viability that are based on the spatial arrangement of habitat patches, habitat quality within and between patches, demographic rates, and dispersal (Akçakaya and Atwood, 1997; Haines et al., 2006). By linking demography to habitat in a spatial framework, metapopulation analytical tools allow scenario assessments such as gauging the relative effect of one management activity vs. another on viability. However, these approaches require an abundance of data that are difficult to obtain, especially in the case of rare, cryptic species such as many endangered carnivores.

While there has been much recent progress in understanding wolverine distribution and ecology in the contiguous US (Cegelski et al., 2006; Copeland et al., 2010; Inman et al., 2012a; Ruggiero et al., 2007; Schwartz et al., 2009), habitat-related tools remain coarse and estimates of potential or current population size do not exist. It is also unclear which patches of wolverine habitat in the contiguous US are capable of female interchange, male interchange, or both. A better understanding of the capacity of areas of historical distribution that remain unoccupied and the degree to which they are likely to be naturally recolonized would aid decisions on whether reintroductions are warranted and, if so, which areas to prioritize. Without a more complete understanding of the spatial arrangement of habitats, their function for wolverines, and potential population numbers therein, these and other metapopulation-level conservation priorities will remain undefined, leaving a host of agencies and conservation organizations without clear roles in what must be a coordinated effort across a vast geographic area (Inman et al., 2012a).

Our objective was to develop a metapopulation framework for wolverines at the scale necessary to conserve the species in the western contiguous US. To do this we: (1) modeled relative habitat quality at the level of species distribution; (2) identified areas suitable for specific wolverine uses that are biologically important and valuable for management purposes (survival, reproduction, dispersal); and (3) related population size to predicted habitat quality in order to estimate potential and current distribution and abundance. We then use this information to identify spatially-explicit population-level conservation priorities across jurisdictions for this candidate threatened or endangered species.

2. Study area

Our field research occurred in the Yellowstone Ecosystem of Idaho, Montana, and Wyoming at approximately 45° north latitude (Fig. 1). Elevations in the study area ranged from 1400 to 4200 m. Precipitation increased with elevation and varied from 32 to 126 cm per year (National Oceanic and Atmospheric Administration, 2007). Snow usually fell as dry powder and depths at higher elevations were often in excess of 350 cm. A variety of vegetative communities were present (Despain, 1990). Low-elevation valleys contained short-grass prairie or sagebrush communities. The lower-timberline transition to forest occurred with lodgepole pine (*Pinus contorta*) or Douglas fir (*Pseudotsuga menziesii*). Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) became more common with increasing elevation. Mixed forest types were common and all forest types were interspersed with grass, forb, or shrub meadows.

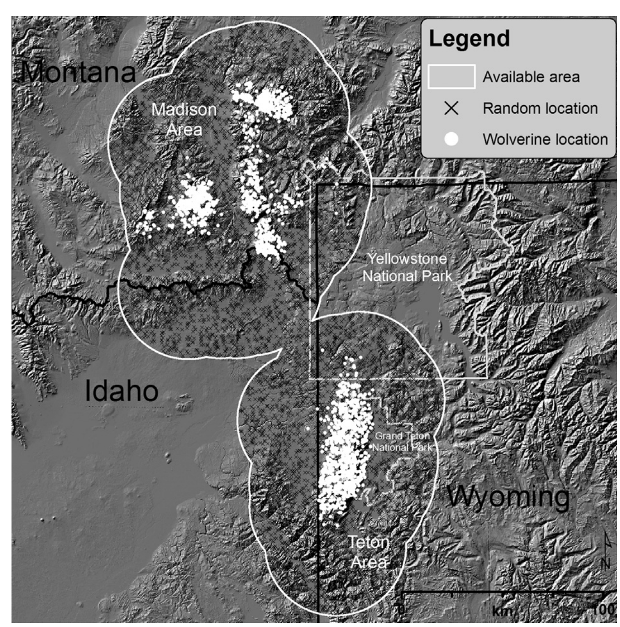

Fig. 1. Locations of wolverines (solid circles) and random points (x's) used to develop a resource selection function model of first order habitat selection, Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010.