

From: [Jeff Copeland](#)
To: [Grizzle, Betty](#)
Subject: Re: FWS request for information re wolverine listing
Date: Sunday, January 15, 2017 11:57:41 AM
Attachments: [Copeland et al. Social ethology of the wolverine.pdf](#)

Also, attached is the *in press* version of our wolverine sociality book chapter. Hopefully, this thing will get published this year. Please don't distribute.

Following is a citation for it if needed:

Copeland, J. P., Landa, A., Heinemeyer, K., Aubry, K. B., van Dijk, J., May R., Persson, J., Squires, J., and Yates, R. (in press). Social ethology of the wolverine. In:

Biology and Conservation of Wild Musteloids. Eds. Macdonald, D.W., Newman, C. and Harrington, L.A. Oxford University Press.

On Sun, Jan 15, 2017 at 11:41 AM, Jeff Copeland <jcopeland224@gmail.com> wrote:

Hello Betty,

Can't tell you how much I enjoyed our phone visit last week. Made me very comfortable to know you are doing this wolverine assessment.

Attached are 2 shapefile files of our wolverine den locations in Idaho from the 1990's study and our Glacier Park dens from the 2000's. Hope this helps your efforts. I'm sure it goes without saying to please not share these data beyond your needs.

Best regards,

Jeff

On Thu, Jan 5, 2017 at 11:25 AM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

Thanks Jeff. Yes, next week if fine. I have received some location data from other National Forests (e.g., Washington), but we have not yet sorted through all of the information received.

In general, I am using the information to construct a wolverine distribution/range map, as we did not present this in our earlier proposed rule. With our new process, preparing/writing a Species Status Assessment Report, we have the opportunity to present this information using maps, thus, my request for spatial coordinates for the observations. However, the maps presented in the Report will be at a scale such that the general public will not be able to easily identify specific points on the ground, but the data layers used will contain those coordinates.

At this point in time we are working through a deliberative process with the wolverine listing determination, and I cannot say exactly what type of additional analysis I will be preparing. For other listing determinations, I have used location data and other information to develop a habitat suitability model (for example, using various GIS procedures).

I hope that answers your question related to my request for information.

Betty

On Wed, Jan 4, 2017 at 3:30 PM, Jeff Copeland <jcopeland224@gmail.com> wrote:

Hello Betty,

Certainly, I would be happy to provide you with den location data. I should probably confirm this with the Forest Service's Rocky Mountain Research Station since they are the "owners" of some of the den points but I can't imagine it being a problem as these should be public data. We tended to keep these data confidential as we didn't want the public using the data to physically visit the den sites but it has been long enough that it shouldn't be a problem.

As I am sure you are well aware, we do like to have some control, or input, into how our data are used and/or presented so may I ask how the data will be used. Also, I have a medical thing going on that will put me down for a day or so, so it may be the end of the week or early next week before I can get everything together and to you. Is that okay?

Jeff

On Wed, Jan 4, 2017 at 3:39 PM, Grizzle, Betty <betty_grizzle@fws.gov> wrote:

Thank you Mr. Copeland for your comments.

I am working with GIS staff in our office to pull together records (particularly den locations) for wolverine observations/occurrences in the lower 48 states. I understand these data will be a mix of survey methods, survey effort, etc., over many years.

My question/request to you: Do you have observation records in GIS format that you can share with the Service? (with the caveat that we may not be able to hold this information confidential)

My contact information is listed below if you have questions.

Thanks again for your time,

Betty

On Fri, Dec 30, 2016 at 10:09 AM, Jeff Copeland <jcopeland224@gmail.com> wrote:

Hello Betty,

Please find attached my comments regarding the FWS's information request. My comments include some new information but are primarily meant to correct gross misinformation provided by Montana Fish Wildlife and Parks in their Oct 17 letter.

Thank you for the opportunity to input and for making my comments a part of the official record.

Best regards,

Jeff Copeland

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SOCIAL ETHOLOGY OF THE WOLVERINE

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Introduction

The wolverine (*Gulo gulo*) is generally known for its wide ranging behavior and association with remote boreal forests and arctic tundra in the northern hemisphere (Pasitschniakk-Arts and Larivière 1995, Copeland and Whitman 2003). The wolverine's large feet, plantigrade locomotion, and compact body are all considered adaptations to a cold, snowy environment (Haglund 1966). Wolverines are sexually dimorphic in size (\bar{x} = 14.1 kg males (N=179), \bar{x} = 10.4 kg females (N = 166) (Landa & Skogland 1995, Landa unpublished data) (Copeland and Whitman 2003) and active throughout the year. A relatively long-lived species with a low reproductive rate, wolverines occur at low population densities and have evolved as a generalist predator and facultative scavenger (van Dijk et al. 2008a,b, May et al. 2008, Mattisson et al. 2011). While New World wolverines often exist undetected, their Old World counterparts are important management species due to their depredation on livestock (Landa et al. 1999, Hedmark et al. 2007, Persson et al. 2006, 2009).

Studies conducted during the last 30 years in Scandinavia and western North America have revealed a fundamental understanding of wolverine spatial use, habitat relationships, demography, and livestock depredation. The social organization of the wolverine has, however, received little attention from researchers (Dalerum 2005) beyond characterizing it as a polygynous carnivore that exhibits intra-sexual territoriality, based primarily from patterns of broad-scale spatial use (Copeland and Whitman 2003).

Recent advances in satellite-based telemetry systems (GPS and Argos transmitters) are enabling researchers to monitor individual wolverines on a spatio-temporal scale unachievable with conventional VHF telemetry systems of the past.

These technologies are revealing previously undisclosed associations between wolverines, although these observations have largely been treated as anecdotal. Here, we compile observations of social interactions from multiple wolverine field studies, and integrate them within their ecological contexts to reveal a complex social organization driven by variable resource availability within extremely large territories that enhances offspring development and survival.

Social behavior in solitary carnivores has long been an active area of investigation (Powell 1979, Macdonald 1983, Sandell 1989, Gittleman 1989, Erlinge 1995, Johnson et al. 2000) but remains largely founded in conjecture compared to our understanding of sociality in group-living species, most likely owing to the more apparent significance and observability of social interactions for species that live in groups. While sociality is commonly considered a group process (Crook 1970) the terms “solitary” and “social” are not mutually exclusive (Charles-Dominique 1977, Waser and Jones 1983, Creel and Macdonald 1995). The former refers to the spatial distribution of animals relative to each other, and not necessarily to their patterns of social interaction (Waser and Jones 1983, Creel and Macdonald 1995). Unfortunately, life history metrics, which are more easily quantified than ecological variables, poorly reflect the complexities of social behavior (Johnson et al. 2000, Creel and Macdonald 1995).

The distinction between classical and social ethology elucidated these complexities by recognizing the dynamic nature of carnivore social organization and the variation in behavior that can result from local environmental variation (Crook 1970, Kawamichi et al. 1987, Schropfer et al. 1997, Wolf 1997, Macdonald 1983, Johnson et al. 2000). Recognizing the ecological basis of social organization (Crook 1970, Macdonald 1983)

requires knowledge of the ecological and social pressures operating on each sex (Rubenstein and Wrangham 1986). This involves looking beyond spatial use patterns and mating systems, and considering other kinds of social interactions (Rubenstein and Wrangham 1986), such as male parental care and sibling associations, that may facilitate learning and increase survival rates.

Ecological Framework for Wolverine Social Ethology

Distribution and habitat associations

The wolverine occurs across the northern latitudes of Eurasia and North America with populations extending south into northern Mongolia, northwestern China, and the northwestern contiguous U.S. Wolverines are associated with the tundra/boreal biome, and generally occur above 50°N latitude in much of its worldwide range. North of 55°N latitude, suitable wolverine habitat is largely ubiquitous in the tundra and boreal forests of northwestern North America (Copeland et al. 2010). Fennoscandian wolverines reside within high elevation alpine tundra habitats of Sweden, Norway and northern Finland and within the boreal forest of central and eastern Finland (Flagstad et al. 2003, Koskela et al. 2013). In North America, wolverines currently occur south to ~45°N latitude along a peninsular extension of subalpine habitat in the western contiguous U.S. (Aubry et al. 2007, Copeland et al. 2010). This high-elevation region contains wolverine habitat that is naturally fragmented and limited in extent, thereby increasing the likelihood of genetic isolation. Suitable high-elevation habitat islands within a lower-elevation matrix result in a naturally discrete population distribution; only connected through extensive dispersal events.

Movement ecology

Wolverines occupy sizable home ranges (male range 382-1246 km², female range 104-963 km²) that notably exceed a magnitude in size greater than would be predicted by body size (McNab 1963, Harestad and Bunnell 1979, Lindstedt et al 1986, Landa et al. 1998, Persson et al. 2010), and occur at exceedingly low densities (2.2-15.4/1,000 km²) (Hornocker and Hash 1981, Copeland and Whitman 2003, Golden et al. 2007, Inman et al. 2012a). Wolverines are renowned for their tendency to move along regularly traveled routes (Munro 1945, Makridin 1964, Haglund 1966), suggesting that their movements are directed toward particular destinations (Copeland 1996) (Fig. 1). Long distance movements are not unusual with average daily movement distances of 12-17 km (Inman 2012b, J. Copeland unpublished data) as wolverines move to and from widely dispersed foraging sites (Fig. 1); two resident male wolverines in Glacier National Park traveled an average of 147 km/week even though they averaged 79% of their time largely inactive at foraging sites, resting sites, or reproductive dens (J. Copeland unpublished data). This destination-driven movement pattern defined by dispersed sites connected by a network of paths aligns closely with Leyhausen's (1963) more precise definition of a home range as an area encompassing specific use sites connected by pathways with the remainder of the enclosed area seldom or never used.

Food habits

During winter months, the wolverine forages primarily on widely distributed animal carcasses (carrion), such as semi-domesticated reindeer (*Rangifer tarandus*), and

wild cervids and bovids, but may also prey opportunistically on small mammals and large ungulates (Mattisson et al. 2011; van Dijk et al. 2008a,b; Lofroth et al. 2007; Landa et al. 1997). Percent occurrence of large ungulates in the wolverine's diet varied from 58% to 84% (Landa et al 1997; Lofroth et al. 2007; van Dijk et al. 2008b; Dalerum et al. 2009; Inman and Packila 2015). Ungulate mortalities in wolverine habitat may occur prior to the onset of winter, often by fatal wounds inflicted by hunters (Copeland 1996), and also during winter from natural causes, or wolverine predation on winter-stressed ungulates (Lofroth et al. 2007). Predation on reindeer made vulnerable by deep, crusted snowpacks is not uncommon in Scandinavia (Landa et al. 1997). Predation by grey wolves (*Canis lupus*) on ungulates may also provide scavenging opportunities for wolverines (Lofroth et al. 2007, van Dijk et al. 2008, Koskela, et al. 2013) in regions where the two species are sympatric during the winter months. Small rodents, hares (*Lepus spp.*), and ground-nesting birds can also be important prey items during the winter (Landa et al. 1997), but may be essential for providing the nutrition needed by females during the early spring and summer to successfully raise their offspring (Landa et al. 1997, Persson 2005, Lofroth et al. 2007, Inman and Packila 2015).

Reproduction and offspring dependence

Mating occurs in mid-summer (Mead et al. 1991), ovulation is induced by coitus (Mead et al. 1993), and implantation of the embryo is delayed (Wright and Rausch 1955). Nidation occurs most commonly in January or February, followed by active gestation lasting 30-40 days (Mead et al. 1991). The solitary female wolverine gives birth to 1-4 offspring from late February to mid-March (Landa et al. 2000, Magoun & Copeland

1998), in a secure snow den beneath deep or drifted snow that is typically associated with natural subnival cavities in boulder talus or beneath fallen trees (Magoun and Copeland 1998, May et al. 2012). Copeland et al. (2010) investigated 562 wolverine den sites in North America and Fennoscandia and found that all were associated with deep snow that persisted into spring. They and others have speculated that denning habitat may be limited (Inman et al. 2012a, Landa et al. 1998), and that deep-snow sites are selected as a mechanism for predator avoidance and for thermal advantage it provides developing offspring (Magoun and Copeland 1998, Persson et al. 2006, May et al. 2012). However, there is little information available on fine-scale environmental factors that influence den site selection (May et al. 2012), or how den selection may influence offspring survival (Persson 2003). High elevation den sites are often located far from food resources (Copeland 1996), indicating that readily available food may not be a primary determinant of den site selection. Females commonly travel 3-5 km from den sites to forage, and have been documented traveling as far as 16 km on such forays (Copeland 1996).

Wolverines appear to have a greater reproductive potential than telemetry studies indicate (Copeland and Whitman 2003). Reported pregnancy rates from trapper-collected carcasses for adult (> 2-years-old) female wolverines varied from 73.4% (Banci and Harestad 1988) to 92% (Rausch and Pearson 1972). Females in the yearling age class rarely produce offspring (7.4% pregnancy rate, Banci and Harestad 1988). Persson et al. (2006) found no reproduction in 2-year-old females ($n = 11$) concluding that the average age at first reproduction was 3.4 years. However, average fecundity (measured by recruitment of post-weaning age offspring) varied from 0.43 (Krebs and Lewis 1999) to 0.89 (Copeland 1996) offspring per adult female suggesting notably lower levels of

recruitment than pregnancy rates. Whether this represents a normal level of attrition for wolverines, or is the result of fetal resorption driven by energetic limitations (Banci and Harestad 1988, Persson et al. 2006), is unclear. Additionally, intraspecific predation was identified as the primary cause of death (50%; $n = 11$) in a Scandinavian study of juvenile wolverine survival (Persson et al. 2003). All instances of intraspecific predation on juveniles occurred post-weaning, with 7 occurring from May to July and 4 occurring from August to September.

Socio-spatial structuring

Investigations of sociobiology in musteloid carnivores has received modest effort (Powell 1979, Macdonald 1983, Sandell 1989, Gittleman 1989, Erlinge 1995, Johnson et al. 2000) with social structuring most commonly inferred from investigation of spatial organization, insofar as it can be deduced from the juxtaposition of home ranges. This has led to intrasexual territoriality as the most accepted spatial model for this group of carnivores, with some exceptions (Powell 1979), with individuals rarely reported associating outside periods of propagation (Leyhausen 1965, Powell's 1979). Space use in this group supports Powell's (1979) hypothesis that the distribution of food determines female home ranges, whereas the distribution of females controls male home ranges. This strategy tends to produce seasonal territory stability when males monopolize access to females within an established territory (Arthur et al. 1989, Balharry 1993), and instability when males chose a roaming strategy to compete for female access (Erlinge and Sandell 1986, Sandell 1989).

Sandell (1989) considered a carnivore species to be “social” if there were cooperative interactions among members of the population that enhanced foraging efficiency, mating success, and predator defense; accordingly, few mustelids were considered to be social. A notable exception was Genovesi and Boitani’s (1997) work on the social ecology of the stone marten (*Martes foina*). They found the spatial ecology of the stone marten to be consistent with Powell’s (1979) intrasexual territoriality model while incompatible with Sandell’s (1989) conclusion that a threshold density exists wherein a male may shift from a roaming to an exclusive range mating system with increasing female density. Male stone marten studied by Genovesi and Boitani (1997) occurred at densities not much greater than that of females suggesting an advantage should be gained by employing a roaming strategy (Sandell 1989). This was not the case as their males displayed limited seasonal variation in territory size suggesting adherence to an exclusive territory strategy. Supported by anecdotal instances of kin association they concluded that the limited seasonal variation in territory size was related to male parental investment and its contribution to increased offspring survival. They argued that the observed spacing pattern could be explained by mating pair familiarity, which might reduce incidence of intraspecific aggression, and hypothesized male parental investment through food provisioning, defense against conspecifics and other predators, and training of young. Genovesi and Boitani’s (1997) model, with its inclusion of male parental care and increased mating pair familiarity stands alone among reported marten socio-spatial strategies while bearing similarity to what we report herein for the wolverine.

Wolverine home range spacing reflects a polygynous mating system (Hedmark et al. 2007) and intrasexual segregation within resident adults (Copeland and Whitman

2003). A resident male will generally associate with 1-4 females (Hedmark et al. 2007,
Copeland and Whitman 2003). Wolverines reside within home ranges that are
intrasexually exclusive between females (Copeland and Whitman 2003), however,
Copeland (1996) found an average overlap of 16% ($n = 4$, range=2.0-26.9) among
neighboring adult males in central Idaho, while others reported overlap as low as 2.1%
(Inman et al. 2012b). Sandell (1989) argued that home ranges should be maintained
without overlap where males adopt a non-roaming reproductive strategy but our inability
to clearly define the wolverine's breeding season has hindered attempts to measure
seasonal variation in home ranges. Early studies suggested increases in male home
ranges and movements during spring and summer related to breeding activity (Hornocker
and Hash 1981, Magoun 1985, Banci 1987) while others reported the opposite (Landa et
al. 1998, Copeland 1996). Whether male wolverines adopt a roam or stay-at-home mate
competition strategy (Sandell 1989) may not be well defined, but one would expect
multiple paternity as a common outcome with the former strategy. In addition,
arguments that male wolverine home ranges may be too large for resource defense
(Koehler et al. 1980, Copeland 1996) gained support with findings that wolverine
offspring were rarely sired by individuals other than the established resident male
(Hedmark et al. 2007). Most competition for mates likely comes from transient males
that are not defending a home range. These individuals move about the landscape vying
for opportunities to breed, displace infirm males, or compete for vacant home ranges.

Male parental association at den sites

Documentation of male parental visits to reproductive dens has increased with the number of field studies. North American researchers tracked 6 male wolverines that were associated with reproductive females, and documented the presence of 4 of these males at or within a few hundred meters of reproductive dens on 14 occasions (Table 1). An individual male in northern Norway was documented visiting his offspring at their reproductive den on 5 occasions during April-May. In June he still visited his family twice at rendezvous sites. Concluding that a male visited a reproductive den required either a visual observation of the male at the den, or a GPS data track and activity sensor data that revealed the male passing by the den and remaining nearby for a longer period of time than that between programmed GPS fixes. In cases where the male was instrumented with a GPS collar, the average duration of these visits was 4.5 hours ($n = 9$, $SD = 3.9$, range = 0.2-12.0). In all cases, the male was confirmed genetically to be the father of the offspring (J. Copeland and K. Heinemeyer, unpublished data). Consequently, male visitations at reproductive dens, which appear to be largely congenial, represent a striking departure from our previous view of parental involvement by male wolverines.

Associations away from the den site

Weaning of juvenile wolverines occurs approximately 10 weeks after parturition (late April to mid-May; Iversen 1972, Magoun and Copeland 1998), followed by a dependency period during which the adult female leaves the offspring at rendezvous sites while she forages for food (May et al. 2010, Magoun and Copeland 1998). Data on the amount of time and the distance the mother spends away from her offspring is sparse, but

such forays can exceed distances of 8 km for >6 hours (Copeland 1996). By the autumn of their first year, the offspring separate from their mother and begin to separate from each other. Scandinavian researchers studied 13 adult females and their 29 offspring, and found that mother/offspring separation occurred 180-195 days after parturition, when offspring were approximately 7 months of age. On average, male offspring separated from their mothers 2 weeks earlier than female offspring (A. Landa, unpublished data). In North America, separation of mothers from their offspring occurred 169-243 days after parturition (mid-August to early October) (Copeland 1996).

For wolverine offspring, the time when they are no longer dependent on their mother doesn't necessarily mark the beginning of their independence nor the initiation of dispersal. In some instances the young wolverine will remain within its natal area (its father's home range) throughout its subadult year, during which time it may associate with its father, mother and/or siblings (Copeland 1996). During the past 20 years, wolverine researchers have noted instances of association (wolverines observed in groups of 2-4 individuals) occurring outside the period when one might expect mating-related grouping. A compilation of these records ($n = 88$), from 5 research projects (Copeland 1996, and unpublished data from K. Aubry, J. Copeland, A. Landa, and K. Heinemeyer) revealed interactions between father and offspring ($n = 39$), out-year siblings and cousins ($n = 5$) and rarely, between nonrelated individuals ($n = 3$) (Table 1). Little information was available on the duration of these associations although Copeland (1996) reported several instances of individuals travelling together for hours at a time and, in some cases, for several days.

Most interesting were instances of father/subadult offspring association that occurred subsequent to the juvenile's separation from their mother, typically early in the offspring's second year (Table 1). This was first noted when a yearling female appeared to become habituated to a live-trap in central Idaho. After approximately a week of capturing her nearly every day, her father arrived at the trap and soon left the area with her at his side. They traveled together for 4 days visiting various foraging sites, and were located together 12 times during the winter (Copeland 1996).

Dispersal and philopatry

Wolverines began making exploratory movements outside their natal area as early as 7 months-of-age (Vangen et al. 2001). Such forays were noted in 25% of Scandinavian wolverines (Vangen et al. 2001) and increased in frequency through the sub-adult year; by 20 months-of-age, most activities were occurring outside of their natal areas (Copeland 1996, Vangen et al. 2001). In many instances exploratory movements immediately preceded dispersal (Copeland 1996, Vangen et al 2001). Copeland (1996) noted males making brief returns to their natal areas as late as 28 months-of-age, and from distances as great as 100 km. Dispersals exceeding 100 km are not uncommon in wolverines; most long-distance dispersals are by males (Gardner et al.1986). Dispersals that involve relatively short-distance shifts into neighboring home ranges that were vacated due to mortality or displacement occur in both sexes, but appear to be most common among females (Aronsson 2009, Gardner et al. 1986). The wolverine's capacity for long-distance movements likely enables the species to (re)colonize gaps in their distribution (Vangen et al. 2001).

Towards an Ethological Framework for Wolverine Sociality

Social behavior is a component of spacing which derives in large part from density and is influenced by local ecological conditions (Clutton-Brock and Harvey 1978, Davies, 1991, Schropfer et al. 1997, Johnson et al. 2000). To be a social carnivore generally means to live in a group (Gittleman 1989) that includes more than 2 adults of the same sex (Johnson et al. 2000); however, it has also been defined as simply acting cooperatively with conspecifics (Balharry 1993, Sandell 1989). Social (or group) living may have evolved as a strategy to better exploit available food resources and avoid predation (Gittleman 1989, Creel and Macdonald 1995), but it may also facilitate the development of offspring (Gittleman 1989) and increase their survival rate (Kleiman and Malcolm 1981, Gubernick and Teferi 2000).

The mating and social strategy for the wolverine is distinguished by three general conditions: a) a single-male polygynous mating system that derives from mated pair familiarity, b) male parental association with and participation in rearing young, c) extended tolerance of subadults, allowing for adequate resources. Clutton-Brock (1991) defined such as facultative polygyny or monogamy depending on the number of females involved. As an intermediate between polygyny and facultative monogamy Genovesi and Boitani (1997) defined the mating strategy of a stone marten population that displayed a similar character as “paternal-investment polygyny.”

a) Single-male polygynous mating system that derives from mated pair familiarity

If familiarity is required for successful mate pairing it might lessen the need for the resident male wolverine to physically defend his associated females against

encroachment by other males. Avoidance of mate competition may also function as compensation for reductions in mating opportunity (Genovesi and Boitani 1997). In this way, territoriality serves to defend the area rather than the mate so that the territory will support the needs of all the females and their offspring. Once attained, this dominance status provides the male with what Eisenberg (1981) termed “priority of access” to resident females resulting from established pair-bonding. In turn, the male provides offspring with additional security during the months of highest vulnerability and his association with offspring after independence from their mother but prior to dispersal may help them develop foraging skills.

b) Male parental association with and participation in rearing young

Male parental investment includes all behaviors by males (whether their effects are direct or indirect) that increase a pre-reproductive mammal’s fitness (Kleiman and Malcolm 1981). The presence of the resident male wolverine and his residual odor at reproductive dens (Table 1) may increase offspring survival indirectly by deterring predators (including conspecifics), particularly when the female is away from the denning area. It may also strengthen the pair bond between the male and female in preparation for mating while developing a social bond between the father and his offspring, which may also help prevent agonistic interactions during later encounters (direct investment) between the father and his male offspring. Furthermore, paternal investment in offspring might be equivalent to alloparental care as a mechanism for reducing the energetic costs of reproduction (Creel and Macdonald 1995); reported variations in reproductive success (Persson et al. 2006) may relate to varying levels of male parental care.

c) Extended tolerance of subadults, allowing for adequate resources

Development toward independence in the young wolverine begins in response to the female's need to leave the offspring so she can forage and mate and the offspring's need to develop survival skills. This occurs from the altricial denning period through the offspring's first summer, at which time they are generally considered to be both nutritionally and socially independent. Waser and Jones (1983) define independence as beginning when offspring cease to forage in spatial association with the mother. They recognized, however, that the timing of nutritional independence for offspring may not reflect their independence from social interactions among close relatives. Developing their survival skills after nutritional independence, including hunting skills and securing food during their first winter, may be facilitated by a tolerance of, and by, conspecifics. Winter food for the wolverine most commonly occurs in the form of carcasses of large ungulates, which represent an abundant and long-lasting, albeit widely dispersed, resource (van Dijk et al 2008a, 2008b, Mattisson et al. 2011). Increased social tolerance appears to be selected in situations where food is concentrated into rich but widely dispersed patches (Kleiman 1977); a situation which Kleiman and Malcolm (1981) believe may have helped foster the evolution of male parental care. While the resident male's tolerance of immature wolverines may vary with food abundance, such interactions could function to facilitate learning and promote the development of survival skills in the relatively few offspring that are produced. Variation in timing of wolverine dispersal is evident throughout the wolverine literature (Copeland 1996, Vangen et al. 2001, Inman et al. 2012a), and is most likely related to food availability, which Vangen et al. (2001) felt was in

keeping with the resource-dispersion hypothesis (Macdonald 1983, Macdonald and Johnson 2015).

The role of resource dispersion in shaping wolverine spacing and philopatry

The resource dispersion hypothesis proposes that in an environment where food resources are patchy, a species' basic social unit (which may be an individual, or most likely a pair or group) will defend a large enough area to be certain that at least one ripe patch will be available to satisfy its (their) resource requirements over a given period of time (Macdonald and Johnson 2015). And, that this area will be large enough to have sufficient, or excess, resources allowing at least minimal provisions to secondary occupants. This latter proposition likely helps explain the wolverine's observed lack of fit to an allometrically scaled home range size (Johnson et al 2000). Given that resource patches occur at a certain probability of availability, several must be simultaneously defended in order to assure availability for the primary residents (Macdonald and Johnson 2015). Wolverine researchers have long noted the wolverine's winter tendency to secure multiple, seemingly excessive, food caches across a broad spatial network. Also, as predicted by the resource dispersion hypothesis, years with good resource availability allow offspring to remain in the natal area while young must disperse early when prey availability declines (Vangen et al. 2001).

In addition to insuring increased survival of the relatively few offspring that are produced, paternal-investment polygyny would also work to maintain long term population stability that can be critically important in low density species. By reducing

the incidence of multiple paternity the population can avoid increasing variance in male reproductive success, which tends to result in a decreasing effective population size (Hedmark et al. 2007, Karl 2008).

Conclusions and Conservation Implications

Across their world-wide range, wolverines occur at low densities and occupy large intrasexually segregated home ranges; both of which encourage a stay-at-home mating strategy for males (Sandell 1989), which in turn may foster familiarity, or pair-bonding between mated pairs and as such, a greater adaptive advantage in male parental care of the few offspring that are produced. This leaves the male with the necessity of bonding with one or several partners followed by a lifetime of defense of resources (territory) and offspring. We propose that this represents a fundamental, if not obligate, mating strategy for wolverines that is consistent with parental-investment polygyny (Genovesi and Boitani 1997), regulated by resource dispersion and, ultimately, potentially susceptible to anthropogenic disruption via harvest and habitat intrusion.

Wolverine populations, particularly those that occur in naturally fragmented habitat near the southern margins of their range, face a variety of challenges to population persistence. Low population densities coupled with naturally fragmented habitat reduce gene flow and increase wolverine population vulnerability to a variety of stochastic threats. Specific habitat requirements (Aubry et al. 2007, Copeland et al. 2010, Inman et al. 2012b) imply that a changing climate could reduce the availability of suitable habitat (McKelvey et al. 2011) and increase resistance to gene flow (Schwartz et al. 2009) throughout much of the wolverine's range. As habitat patches become increasingly

isolated, the likelihood that vacant patches will become occupied decreases (Sutherland 1998). Responses by dispersing individuals to variation in habitat quality and associated environmental variables can influence their population dynamics (Sutherland 1998, Macdonald and Johnson 2001, Bowler and Benton 2005), and such considerations could become critically important if wolverine habitat becomes increasingly fragmented due to climate change (McKelvey et al. 2011). Artificial recolonization of historical habitat through translocation, which is currently being considered in the western U.S., would benefit from a clearer understanding of wolverine social structure and dispersal dynamics. Furthermore, in areas where wolverines are controlled due to depredation on domestic reindeer or sheep as in Fennoscandia (Landa et al. 2000) or kept at estimated minimal viable population sizes (Sæther et al. 2005) as in Norway, an improved understanding of the wolverine social system may be critical to foreseeing induced turnover effects and their impacts on population dynamics.

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Table 1. Observations of associations between both related and unrelated wolverines, including 10 adult males, 11 adult females, 15 juvenile or subadult females, and 16 juvenile or subadult males. Years 1 and 2 represent the juvenile and subadult years (respectively) of the pre-adult member of the pairing; columns indicate the month in which the association occurred. For observations where age was unknown, we placed the observation in year 2 for convenience.

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Julian day from March 1	Year 1												Year 2												Total			
	31	61	92	122	153	184	214	245	275	306	337	365	M	A	M	J	J	A	S	O	N	D	J	F		M	A	M
	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F		M	A	M
Adult male/female outside mating season																			2				1					3
Male at den (natal or maternal)	12	5	2																								19	
Adult male/female and kits together		3	3	2																							8	
Father/male offspring			1	1					4		5	1	1	1		2							1				17	
Father/female offspring				1			2				2	3	4	1									1				14	
Mother/offspring											4		1										1				6	
Siblings								5	2	2	2																11	
Out-year siblings										2	3																5	
Subadult cousins														2													2	
Subadult/adult unrelated male													1										1				2	
Adult/Adult unrelated																						1					1	
Total	12	8	6	4	0	0	2	5	6	4	12	8	6	3	2	0	2	0	0	2	0	2	4	0	0	0	0	88

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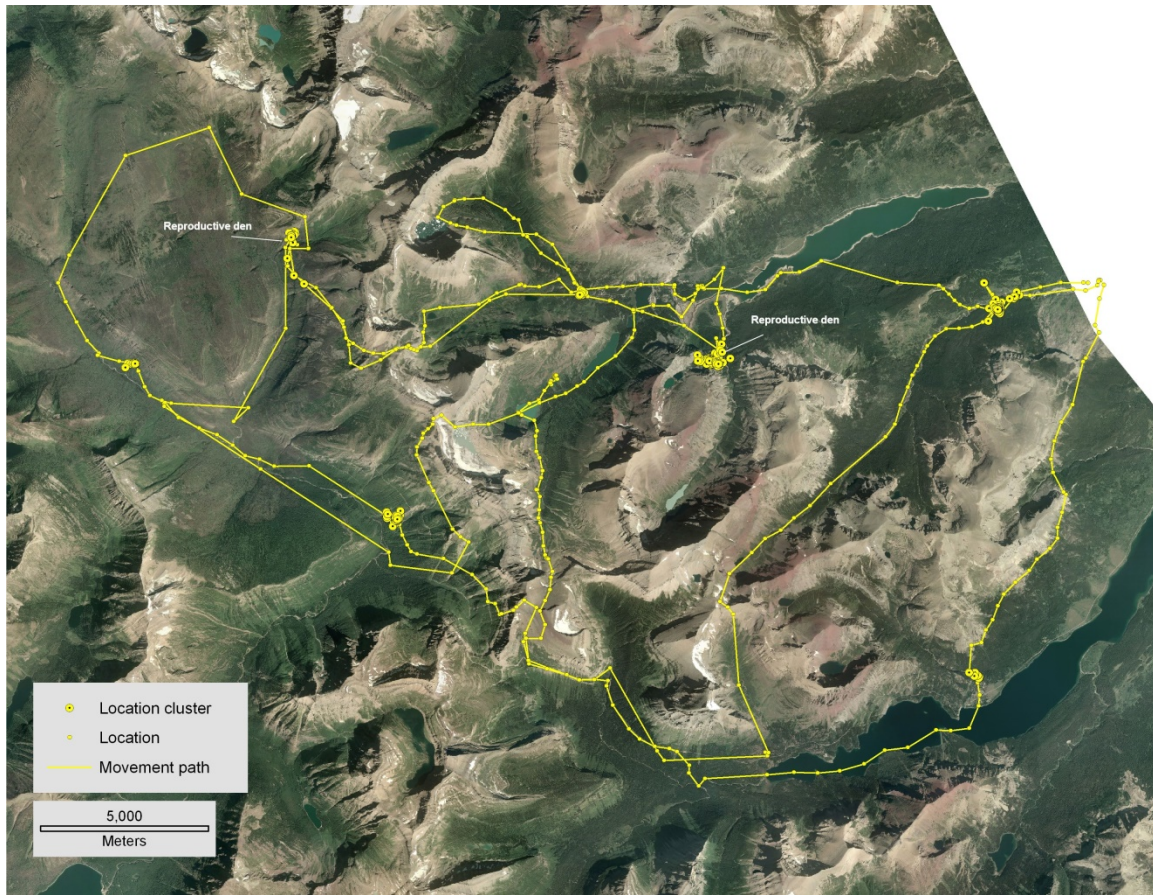


Figure 1. Movement path of an adult male wolverine in 2006. The path was derived from a GPS collar programmed to collect a point every 5 minutes, and represents 8 days of data in March. Duration of stay at clusters ($N = 10$) averaged 10.2 hours ($SD = 13.2$, range = 0.5-37.5 hours). Clusters denote reproductive dens (see inset), foraging and resting sites.