

Corresponding author

Jeffrey P. Copeland
The Wolverine Foundation
4444 Packsaddle Road
Tetonia, ID, USA 83452
Phone: 01-208-994-9156
Email: jpcopeland@wolverinefoundation.org

SOCIAL ETHOLOGY OF THE WOLVERINE

Jeffrey P. Copeland, Arild Landa, Kimberly Heinemeyer, Keith B. Aubry, Jiska van Dijk,
Roel May, Jens Persson, John Squires, and Richard Yates

The Wolverine Foundation, Inc., 4444 Packsaddle Road, Tetonia, ID, USA (JC)

*Norwegian Institute for Nature Research (NINA), P. Box 5695, NO-7485, Trondheim,
Norway (AL, RM, RA, JvD)*

*Grimsö Wildlife Research Station, Department of Ecology, Swedish University of
Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden (JP)*

*Round River Conservation Studies, 284 W., 400 N., Suite 105, Salt Lake City, UT, USA
(KH)*

*USDA Forest Service, Pacific Northwest Research Station, Olympia, WA 98512, USA
(KBA)*

USDA Forest Service, Rocky Mountain Research Station, Missoula, MT, USA (JS, RY)

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in size ($\bar{x}$ = 14.1 kg males (N=179), $\bar{x}$ = 10.4 kg females (N = 166) (Landa & Skogland 1995, Landa unpublished data) (Copeland and Whitman 2003) and active throughout the year.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

203). 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.

Acknowledgements

We wish to thank the many wolverine field technicians that worked so diligently on these studies, and the public agencies and private organizations whose funding support made them possible.

References

- Aronsson, M. 2009. Territorial dynamics of female wolverines. Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden. 40pp.
- Arthur, S. M., Krohn, W. B. and Gilbert, J. R. 1989. Home range characteristics of adult fishers. *Journal of Wildlife Management* 53:674-679.
- Aubry, K. B., McKelvey, K. S., and Copeland, J. P. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71: 2147-2158.
- Balharay, D. 1993. Social organization in martens: an inflexible system? *Symposia of the Zoological Society of London* 65:321-345.
- Banci, V. 1987. Ecology and behavior of wolverine in Yukon. Thesis, University of British Columbia, Vancouver, British Columbia, Canada.
- Banci, V. & Harestad, A. S. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. - *Annales Zoologici Fennici* 25: 265-270.
- Bowler, D. E. and Benton T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Review* 80:205-225.
- Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, New Jersey, USA.
- Copeland J. P. & Whitman, J. S. 2003. Wolverine *Gulo gulo*. Pages 672-681 in *Wild mammals of North America: biology, management, and conservation*. G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Johns Hopkins University Press, Baltimore, Maryland, USA.

452 Copeland, J. P. 1996. Biology of the wolverine in central Idaho. Thesis, University of
 453 Idaho. Moscow, USA. 138pp.

454 Copeland, J. P., McKelvey, K. S., Aubry, K. B., Landa, A., Persson, J., Inman, R. M.,
 455 Krebs, J., Lofroth, E., Golden, H., Squires, J. R., Magoun, A., Schwartz, M. K.,
 456 Wilmot, J., Copeland, C. L., Yates, R. E., Kojola, I. and May, R. 2010. The
 457 bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit
 458 its geographic distribution? Canadian Journal of Zoology 88: 233-246.

459 Charles-Dominique, P. 1977. Ecology and behavior of nocturnal primates. Columbia
 460 Univ. Press, New York.

461 Creel, S., and Macdonald, D. 1995. Sociality, group size, and reproductive suppression
 462 among carnivores. Advances in the study of behavior 24:203-257

463 Crook, J. H. 1970. Social organization and the environment: aspects of contemporary
 464 social ethology. Animal Behaviour 18:197-209.

465 Dalerum, F. 2005. Sociality in a solitary carnivore, the wolverine. Dissertation,
 466 Stockholm University, Sweden.

467 Dalerum, F., Kunkel, K., Angerbjörn, A., and Shults, B. S. 2009. Diet of wolverines
 468 (*Gulo gulo*) in the western Brooks Range, Alaska. Polar Research 28:246-253.

469 Eisenberg, J. 1981. The mammalian radiations: an analysis of trends in evolution,
 470 adaptation and behavior. University of Chicago Press, Illinois, USA.

471 Erlinge, S. & Sandell, M. 1986. Seasonal changes in the social organization of male
 472 stoats, *Mustela erminea*: an effect of shifts between two decisive resources. Oikos
 473 47: 57-62.

474 Erlinge, S. 1995. Social organization in European small mustelids. *Hystrix, the Italian*
475 *Journal of Mammalogy*, 7:1-2.

476 Flagstad, Ø., Hedmark, E. V. A., Landa, A., Brøseth, H., Persson, J., Andersen, R., ... &
477 Ellegren, H. 2004. Colonization history and noninvasive monitoring of a
478 reestablished wolverine population. *Conservation Biology* 18:676-688.

479 Gardner, C. L., Ballard, W., and Jessup, R. H. 1986. Long distance movement by an
480 adult wolverine. *Journal of Mammalogy* 67:603.

481 Genovesi, P., Sinibaldi, I., and L. Boitani. 1997. Spacing patterns and territoriality of the
482 stone marten. *Canadian Journal of Zoology* 75:1966-1971.

483 Gittleman, J. L. 1989. Carnivore group living: comparative trends. Pages 183-208 in J.
484 L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Cornell
485 University Press, Ithaca, New York, USA.

486 Golden, H. N., Henry, J. D., Becker, E. F., Goldstein, M. I., Morton, J. M. Frost, D. Sr.,
487 and Poe, A. J. 2007. Estimating wolverine *Gulo gulo* population size using quadrat
488 sampling of tracks in snow. *Wildlife Biology* 13: 52-61.

489 Gubernick, D. J., and Teferi, T. 2000. Adaptive significance of male parental care in a
490 monogamous mammal. *Proceedings of the Royal Society of London* 267:147-150.

491 Haglund, B. 1966. De stora rovdjurens vintervanor. *Viltrevy* 4: 1-311.

492 Harestad A. S., and Bunnell F. L. 1979. Home range and body weight – a reevaluation.
493 *Ecology* 60:389-402.

494 Hedmark, E., Persson, J., Segerström, P., Landa, A. and Ellegren, H. 2007. Paternity and
495 mating system in wolverines *Gulo gulo*. *Wildlife Biology* 13(Suppl. 2): 13-30.

496 Hornocker, M. G. & Hash, H. S. 1981. Ecology of the wolverine in northwestern
 497 Montana. *Canadian Journal of Zoology* 59: 1286-1301.

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

501 Inman R. M., Magoun, A. J., Persson, J., and Mattisson, J. 2012a. The wolverine's niche:
 502 linking reproductive chronology, caching, competition, and climate. *Journal of*
 503 *Mammalogy* 93:634-644.

504 Inman R. M., Packila M. L., Inman, K. H., McCue, A. J., White, G. C., Persson, J., Aber,
 505 B. C., Orme, M. L., Alt, C. L., Cain, S. L., Fredrick, J. A., Oakleaf, B. J., and
 506 Sartorius. S. S. 2012b. Spatial ecology of wolverines at the southern periphery of
 507 distribution. *Journal of Wildlife Management* 76:778-792.

508 Inman R. M., and Packila M. L. 2015. Wolverine (*Gulo gulo*) food habits in Greater
 509 Yellowstone. *American Midland Naturalist* 173:156-161.

510 Iversen, J.A. 1972. Metabolic rate of wolverines during growth. *Norwegian Journal of*
 511 *Zoology* 20: 317-322.

512 Johnson, D. D. P., Macdonald, D. W., and Dickman A. 2000. An analysis and review of
 513 models of the sociobiology of the Mustelidae. *Mammal Review* 30:171-196.

514 Karl, S. A. 2008. The effect of multiple paternity on the genetically effective size of a
 515 population. *Molecular Ecology* 17:3973-3977.

516 Kleiman, D. G., and J. R. Malcolm. 1981. The evolution of male parental investment in
 517 mammals. Pages 347-387 *in* Parental care in mammals. D. J. Gubernick & P. H.
 518 Klopfer, editors. Plenum Press, New York, USA.

519 Kawamichi, T., Dawamichi, M., and Kishimoto R. 1987. Social organization of solitary
 520 mammals. Pages 173-188 *in* Y. Ito et al., editors. Animal societies: theories and
 521 facts. Japan Scientific Society Press, Tokyo, Japan.

522 Kleiman, D. G. 1977. Monogamy in mammals. *The Quarterly Review of Biology*
 523 52:39-69.

524 Kleiman, D. G., and Malcolm, J. R. 1981. The evolution of male parental investment in
 525 mammals. Pages 347-387 *in* D. J. Gubernick and P. H. Klopfer, editors. Parental
 526 care in mammals. Plenum Press, New York, New York, USA.

527 Koehler, G. M., Hornocker, M. G., and Hash, H. S. 1980. Wolverine marking behavior.
 528 *Canadian Field-Naturalist* 94:339-341.

529 Koskela, A., Kaartinen, S., Aspi, J., Kojola, I., Helle, P., and Rytkönen, S. 2013. Does
 530 grey wolf presence affect habitat selection of wolverines? *Annales Zoologici*
 531 *Fennici* 50:216-224

532 Krebs, J.A., and Lewis, D. 1999. Wolverine ecology and habitat use in the North
 533 Columbia Mountains: progress report. Pages 695-703 *in* *Proceedings Biology and*
 534 *Management of Species and Habitats at Risk*. L. M. Darling, editor. Kamloops,
 535 British Columbia, Canada.

536 Landa, A., Strand, O., Swenson, J. E., and Skogland, T. 1997. Wolverines and their prey
 537 in southern Norway. *Canadian Journal of Zoology* 75:1292-1299.

538 Landa, A., Strand, O., Linnell, J. D. C. and Skogland, T. 1998. Home-range sizes and
 539 altitude selection for arctic foxes and wolverines in an alpine environment.
 540 *Canadian Journal of Zoology* 76: 448-457.

541 Landa, A., Gudvangen, K, Swenson, J. E., and Røskaft, E. 1999. Factors associated with
542 wolverine (*Gulo gulo*) predation on domestic sheep. *Journal of Applied Ecology*
543 36: 963-973.

544 Landa, A., Lindén, M. and Kojola, I. 2000. Action plan for the conservation of
545 wolverines (*Gulo gulo*) in Europe. Report to the Council of Europe Convention
546 on the Conservation of European Wildlife and Natural Habitats Nature and
547 Environment, No. 115. Council of Europe Press, Strasbourg, France, 45 pp.

548 Leyhausen, P. 1963. The communal organisation of solitary mammals. *Proceedings of*
549 *the Symposia of the Zoological Society of London* 14:249-263

550 Lindstedt, S. L., Miller B. J., and Buskirk, S. W. 1986. Home range, time, and body size
551 in mammals. *Ecology* 67:413-418.

552 Lofroth, E. C., Krebs, J. A. Harowwer, W. L., and Lewis, D. 2007. Food habits of
553 wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. *Wildlife*
554 *Biology* 13(Suppl. 2): 31-37.

555 Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379-
556 384.

557 Macdonald, D. W., and Johnson, D. D. P. 2001. Dispersal in theory and practice:
558 consequences for conservation biology. Pages 358-372 *in* *Dispersal*. J. Clobert, E.
559 Danchin, A. A. Dhondt, & J. D. Nichols, editors. Oxford University Press, UK.

560 Macdonald, D. W., and Johnson, D. D. P. 2015. Patchwork planet: the resource
561 dispersion hypothesis, society, and the ecology of life. *Journal of Zoology* 295:75-
562 107.

563 Magoun, A. J. 1985. Population characteristics, ecology and management of wolverines
564 in northwestern Alaska. Dissertation, University of Alaska, Fairbanks, USA.

565 Magoun, A. J. & Copeland, J. P. 1998. Characteristics of wolverine reproductive den
566 sites. *Journal of Wildlife Management* 62:1313-1320.

567 Makridin, B. P. 1964. On the distribution and biology of the wolverine in the Far North.
568 *Zoologicheski Zhurnal*. 43: 1688-1692.

569 Mattisson, J., Persson, J., Andrén, H., and Segerström, P. 2011. Temporal and spatial
570 interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a
571 facultative scavenger, the wolverine (*Gulo gulo*). *Canadian Journal of Zoology*
572 89:79-89.

573 May, R., van Dijk, J., Wabakken, P., Swenson, J. E., Linnell J. D. C., Zimmermann, B.,
574 Odden, J., Pedersen H. C., Andersen, R., and Landa, A. 2008. Habitat
575 differentiation within the large-carnivore community of Norway's multiple-use
576 landscapes. *Journal of Applied Ecology* 45:1382-1391.

577 May, R., van Dijk, J., Landa, A., Andersen, R. and Andersen, R. 2010. Spatio-temporal
578 ranging behaviour and its relevance to foraging strategies in wide-ranging
579 wolverines. *Ecological Modelling* 221:936-943.

580 May, R., Gorini, L. van Dijk, J., Brøseth, H. Linnell, J. D. C., and Landa, A. 2012.
581 Habitat characteristics associated with wolverine den sites in Norwegian multiple-
582 use landscapes. *Journal of Zoology* 287:195-204.

583 McNab B. K. 1963. Bioenergetics and the determination of home range size. *The*
584 *American Naturalist* 97:133-140.

585 McKelvey, K. S., Copeland, J. P., Schwartz, M. K., Littell, J. S., Aubry, K. B., Squires, J.
 586 R., Parks, S. A., Elsner, M. M., and Mauger, G. S. 2011. Climate change predicted
 587 to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological*
 588 *Applications* 21:2882-2897.

589 Mead, R. A., Rector, M., Starypan, G., Neirinckx, S., Jones, M. and DonCarlos, M. N.
 590 1991. Reproductive biology of captive wolverines. *J. Mammal.* 72: 807-814.

591 Munro, J.A. 1945. Preliminary report on the birds and mammals of Glacier National
 592 Park, British Columbia. *Can. Field-Nat.*: 59: 175-190.

593 Pasitschniak-Arts, M., and S. Lariviere. 1995. *Gulo gulo*. *Mammalian Species* 499.

594 Persson, J., Willebrand, T., Landa, A., Andersen, R., and Segerström, P. 2003. The role
 595 of intraspecific predation in the survival of juvenile wolverines. *Wildlife Biology*
 596 9:21-28.

597 Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and
 598 winter food availability. *Canadian Journal of Zoology* 83:1453-1459.

599 Persson, J., Landa, A., Andersen, R. and Segerström, P. 2006. Reproductive
 600 characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of*
 601 *Mammalogy* 87:75-79.

602 Persson, J., Ericsson, G., and Segerström, P. 2009. Human caused mortality in the
 603 endangered Scandinavian wolverine population. *Biological Conservation*
 604 142:325-331.

605 Persson, J., Wedholm, P., and Segerström, P. 2010. Space use and territoriality of
 606 wolverines (*Gulo gulo*) in northern Scandinavia. *European Journal of Wildlife*
 607 *Research* 56:49-57.

608 Powell, R. A. 1979. Mustelid spacing patterns: variations on a theme by
 609 Mustela. *Zeitschrift für Tierpsychologie* 50:153-165.
 610 Rausch, R. A., and Pearson, A. M. 1972. Notes on the wolverine in Alaska and the
 611 Yukon territory. *J. Wildl. Manage.* 36: 249-268.
 612 Rubenstein, D. I. & Wrangham, R. W. 1986. Socioecology: origins and trends. Pages 3-
 613 20 in *Ecological aspects of social evolution*. D. I. Rubenstein & R. W. Wrangham,
 614 editors. Princeton University Press, New Jersey, USA.
 615 Sæther, B. E., Engen, S., Persson, J., Brøseth, H., Landa, A., and Willebrand, T. 2005.
 616 Management strategies for the wolverine in Scandinavia. *Journal of Wildlife*
 617 *Management* 69:1001-1014.
 618 Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores.
 619 Pages 164-182 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and*
 620 *evolution*. Cornell University Press, Ithaca, New York, USA.
 621 Sutherland, W. J. 1998. The importance of behavioural studies in conservation biology.
 622 *Animal Behaviour* 56:801-809.
 623 Schwartz, M. K., Copeland, J. P. Anderson, N. J., Squires, J. R., Inman, R. M.,
 624 McKelvey, K. S., Pilgrim, K. L., Waits, L. P., and Cushman, S. A. 2009.
 625 Wolverine gene flow across a narrow climatic niche. *Ecology* 90: 3222-3232.
 626 van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen,
 627 R., Andersen, R., Steen, H., and Landa, A. 2008a. Diet shift of a facultative
 628 scavenger, the wolverine, following recolonization of wolves. *Journal of Animal*
 629 *Ecology* 77:1183-1190.

630 van Dijk, J., Andersen, T., May, Andersen, R., Andersen, R., and Landa, A. 2008b.
 631 Foraging strategies of wolverines within a predator guild. Canadian Journal of
 632 Zoology 86:966-975.
 633 Vangen, K. M., Persson, J., Landa, A., Andersen, R. and Segerstrom, P. 2001.
 634 Characteristics of dispersal in wolverines. Canadian Journal of Zoology 79:
 635 1641-1649.
 636 Waser, P. M. & Jones, W. T. 1983. Natal philopatry among solitary mammals. Quarterly
 637 Review of Biology 58:355- 390
 638 Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective.
 639 Journal of Animal Ecology 66:1-13.
 640 Wright, P. L., and Rausch, R. 1955. Reproduction in the wolverine (*Gulo gulo*). J.
 641 Mammal. 36: 346-355.

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.

646

	Year 1												Year 2															
Julian day from March 1	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	J	J	A	S	O	N	D	J	F	M	A	M	Total
Adult male/female outside mating season													21												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	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

647

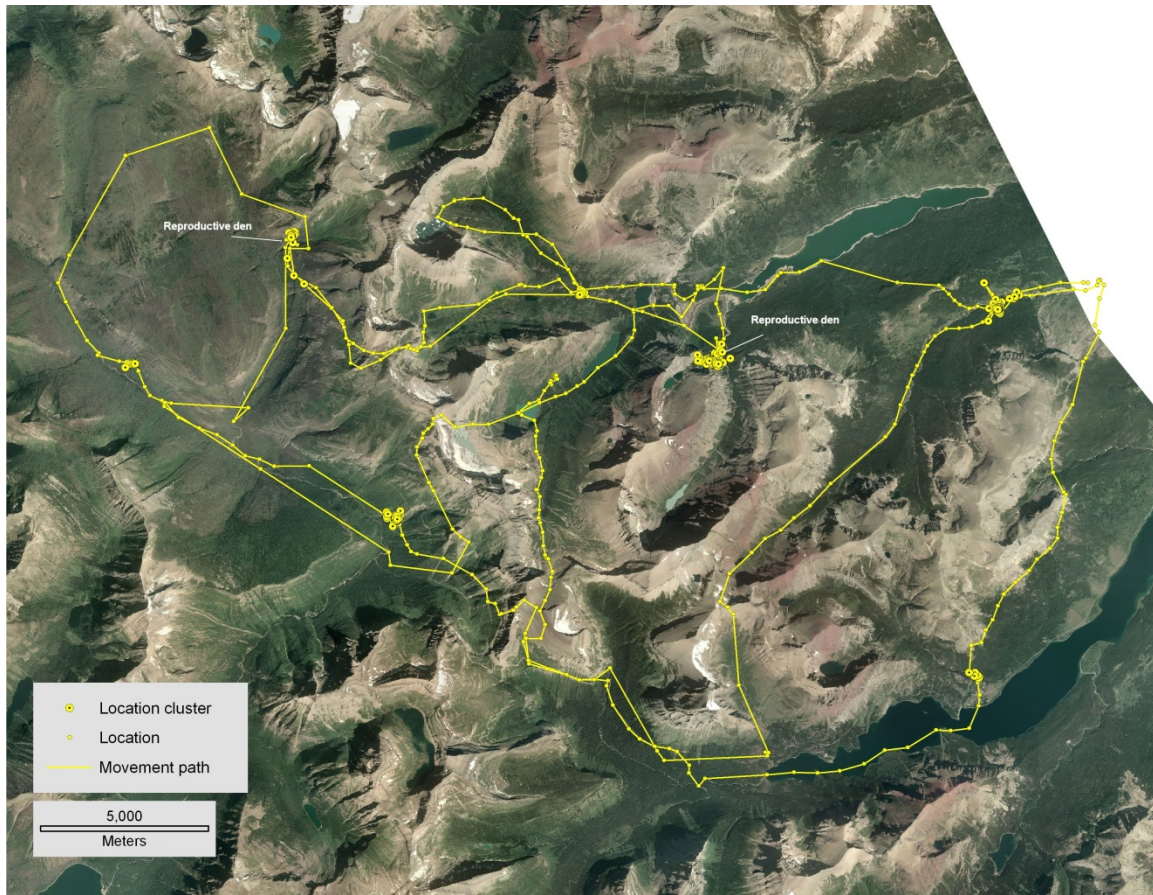


Figure 1. Movement path of an adult male wolverine in 2006. The path was derived from a GPS collar programmed to collect a point every 5 minutes, and represents 8 days of data in March. Duration of stay at clusters ($N = 10$) averaged 10.2 hours ($SD = 13.2$, range = 0.5-37.5 hours). Clusters denote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