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Mismatch between goals and the scale of actions constrains adaptive carnivore management: the case of the wolverine in Sweden

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Abstract

Efficient conservation of wide-ranging carnivores requires that adaptive management consider the varying ecological and societal conditions within the entire range of a population. In northern Europe, large carnivore management has to balance carnivore conservation and maintaining the indigenous reindeer-herding culture. Wolverine *Gulo gulo* monitoring and management in Sweden is currently focused on alpine reindeer husbandry areas where wolverine abundance and associated depredation conflicts have been highest. However, this focus ignores a potential southwards population expansion because current monitoring relies on snow-based tracking methods that are not applicable outside northern alpine areas. Thus, in this study we: (1) used available monitoring data from 1996 to 2014 in Sweden to assess wolverine distribution trends in relation to national management goals, and (2) evaluate the current monitoring protocol against the use of camera stations as an alternative, snow-independent, method for detecting wolverine presence at the southern periphery of its distribution. We show that the wolverine population in Sweden has expanded considerably into the boreal forest landscape, and colonized areas without reindeer husbandry and persistent spring snow cover. The latter indicates a less strict relationship between wolverine distribution and snow cover than previously hypothesized. Current management continues to use a monitoring protocol that is only adapted to high-conflict alpine areas, and is not adapting to changing conditions in the population range, which creates a problematic scale mismatch. Consequently, national management decisions are currently based on incomplete population information, as roughly a third of wolverine's range is not included in official population estimates, which could have detrimental consequences for conflict mitigation and conservation efforts. This illustrates that an important key to successful carnivore conservation is flexible management that considers the entire range of conditions at the appropriate regional and temporal scales under which carnivores, environment and people interact.

Introduction

A common challenge for conservation of natural resources is matching the scales at which actions are planned and implemented to the scale of ecological processes or conservation issues (Cumming, Cumming & Redman, 2006; Guerrero *et al.*, 2013; Hermoso *et al.*, 2016). Scale mismatches can have negative consequences for species' conservation and management of focal species' impacts on ecosystems and human interests (Cumming *et al.*, 2006; Delsink *et al.*, 2013; Creel *et al.*, 2015; Hermoso *et al.*, 2016). As many carnivores range over vast areas the same population could encompass a variety of habitats (Balme *et al.*, 2013; Linnell, 2015). Thus, management conditions may vary within populations because of variation in conflict levels, conflict mitigation systems and environmental conditions (Swenson & Andrén, 2005; Blanco & Cortés, 2011; Linnell & Boitani, 2012). Consequently, carnivore conservation is challenging and requires adaptive management at the appropriate scale in relation to actual conditions and conservation goals (Linnell & Boitani, 2012; Balme *et al.*, 2013; Linnell, 2015). Moreover, additional complexity is added to carnivore management and policy in areas where indigenous communities or traditional practices are affected by carnivores (Lundmark & Matti, 2015).

Because adaptive management requires reliable population estimates to interpret the effects of management actions, a clear link among population monitoring, management actions and population goals is crucial (Walters & Hilborn, 1978). Consequently, monitoring programmes need to be flexible to account for changes in the population's range or environmental conditions to provide updated knowledge on population status. For example, where monitoring of large carnivores has traditionally relied on snow tracking (Landa *et al.*, 1998; Andrén *et al.*, 2002; Liberg *et al.*, 2012*a*), there is an urgent need to adapt monitoring methods to decreased snow cover resulting from global warming and/or population range expansions outside of areas with regular snow.

Due to intense persecution in the 1900s, the Swedish wolverine *Gulo gulo* population was diminished and restricted to northern alpine areas (Flagstad *et al.*, 2004). Today the wolverine distribution largely overlaps with the reindeer husbandry area where semi-domestic reindeer *Rangifer tarandus* are the predominant prey for wolverines (Mattisson *et al.*, 2011). Consequently, wolverines and other predators cause significant economic losses for indigenous Sámi reindeer-herding communities (Hobbs *et al.*, 2012), which necessitates balancing carnivore conservation and sustainability of an indigenous culture (United Nations Declaration on the Rights of Indigenous Peoples, 2008). In 1996, a conservation performance payment system (CPP) was implemented, where reindeer-herding districts are paid in relation to wolverine presence (Persson, Rauset & Chapron, 2015). The unit for payments is yearly number of wolverine reproductive events (hereafter reproductions) and, as wolverines give birth in February–March (Inman *et al.*, 2012), monitoring is mainly based on snow tracking to find den sites in the spring. The CPP has had a positive effect on wolverine female survival, which has contributed to a considerable population increase within the reindeer-husbandry area (Persson *et al.*, 2015). However, losses to predators must not exceed 10% of reindeer numbers in any reindeer-herding district [Swedish Environmental Protection Agency (SEPA), 2014] and lethal control is implemented within the reindeer husbandry area as a conflict mitigating measure to decrease predation pressure (Persson, Ericsson & Segerström, 2009). Consequently, the Swedish national management plan aims to increase wolverine distribution outside the reindeer husbandry area, to be able to reduce depredation conflicts while maintaining the national population goal of at least 600 wolverines (SEPA, 2014).

The political goal to promote a southwards population expansion presents challenges for wolverine conservation in Sweden. Wolverines are hypothesized to be dependent on persistent spring snow cover due to its importance for reproductive success (i.e. den site suitability) and food caching efficiency (Copeland *et al.*, 2010; Inman *et al.*, 2012). Furthermore, the current monitoring programme, and thus population estimates, primarily relies on snow tracking. Thus, snow conditions could limit both the desired southwards expansion of the wolverine population as well as the detection of any southwards expansion through snow-based monitoring methods.

In this study we assess the wolverine population trend in Sweden regarding both population size and distribution in relation to national management goals, as well as the potential need for modification of the current monitoring programme to adequately monitor the desired range expansion. First, we compare monitoring results from different parts of Sweden: (1) inside and outside the reindeer husbandry area and (2) in alpine areas, which have since long been perceived as the typical wolverine habitat in Sweden, relative to the boreal forest landscape both within and south of the reindeer husbandry area (Fig. 1). Second, we conducted a pilot study at the southernmost periphery of wolverine distribution (Fig. 1) where we evaluated if we could document wolverine presence using both the current monitoring methods (see Methods) and an alternative, snow-independent, monitoring method developed for wolverines (i.e. camera stations) following Magoun *et al.* (2011).

Materials and methods

Wolverine monitoring and population estimates

The monitoring programme for wolverines in Scandinavia started in 1996 and is based on annual minimum counts of reproductions (i.e. documentation of active den sites and females with offspring). The monitoring protocol is strictly regulated by the SEPA (www.swedishepa.se) and Norwegian Rovdata (www.rovdata.no; SEPA & Rovdata, 2013*a*,*b*, 2014). Authorized monitoring personnel register wolverine activity in the field from February to June each year (SEPA & Rovdata, 2014). Within the monitoring programme reproductions can be classified as either *documented* or *considered certain* (Anon 2015*a*). A reproduction is classified as *documented* if one of the following criteria is fulfilled: (1) monitoring personnel has photographed wolverine cub/-s or tracks of cub/-s; (2) a wolverine cub is euthanized (i.e. due to lethal control of females with dependent young) or found dead or (3) a lactating wolverine female is captured or found dead (SEPA & Rovdata, 2013*a*). A *considered certain* reproduction represents a lower level of certainty and the criteria are based on repeated wolverine activity and signs indicating that a reproduction has occurred at a suspected den site (see Supporting Information Appendix S1). Suspected den sites are found by snow tracking and most of the criteria for a *considered certain* reproduction are based on snow tracking, however, a suspected den site can also be inspected during early summer (i.e. bare ground investigation) in search for specific signs of repeated activity that can result in the site being classified as a *considered certain* reproduction (see Supporting Information Appendix S1).

For each registered reproduction, coordinates and dates for fulfilment of criteria are stored in the Scandinavian database Rovbase (rovbase30.miljodirektoratet.no) where it is subject to independent quality control by a central coordinator in each country (Anon 2015*a*). Since 2004, in addition to reproductions, validated opportunistic observations of wolverine presence (i.e. visual observations, observations of tracks and collection of DNA from scats) are stored in the database. Scat samples are genetically analysed, and information regarding individual identity and sex are recorded [SEPA & Rovdata, 2013*b*; see Hedmark *et al.* (2004) and Brøseth

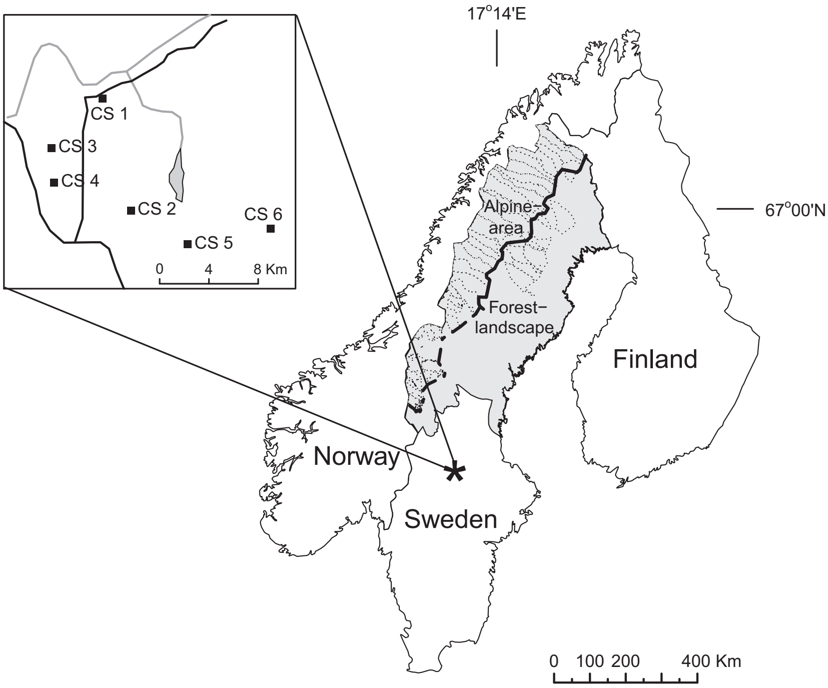

Figure 1 The reindeer husbandry area of Sweden (shaded area) with year-round grazing areas (grey dotted lines). The 'cultivation limit' (black line; cf. Lundmark, 2006; Axelsson *et al.*, 2007) and year-round reindeer grazing areas (black dotted line) differentiate alpine areas and boreal forest landscape in this study. The pilot study of monitoring methods was conducted in the southern periphery of the wolverine distribution (*), placement of camera stations (CS) within the study area is showed in the upper left panel.

et al. (2010) for detailed description of the microsatellite genotyping for sex and individual identity used within the monitoring programme].

National population estimates (i.e. total number of >1-year-old individuals) are calculated each year, using a population model that includes the average number of registered reproductions the last 3 years, sex ratio, age structure and proportion of reproducing females for different age classes (Landa *et al.*, 1998; Brøseth *et al.*, 2010; Anon, 2015*a*). Consequently, annual estimates of population size are based solely on the number of reproductions, not other data (Anon, 2015*a*).

Population trend

To assess changes in wolverine numbers and distribution in Sweden, we used Rovbase data from 1996 to 2014. These data include coordinates for all reproductions from 1996 to 2014 and all other registered wolverine observations from 2004 to 2014. We created a 10-km buffer zone around each location (i.e. to include an area slightly larger than the mean female territory to account for additional individuals; Persson, Wedholm & Segerström, 2010) and merged them to yearly polygons for reproductions and observations, respectively.

The reindeer husbandry area covers 230 000 km^2 of Sweden and is divided into 51 reindeer-herding districts (~50% of land area; Fig. 1) that consist of areas designated for winter-only and year-round reindeer grazing (Hobbs *et al.*, 2012); reindeers are absent south of the reindeer husbandry area. Northern alpine areas have long been perceived as typical wolverine habitat in Sweden (Aronsson & Persson, 2012). To differentiate alpine areas from the boreal forest landscape, we used the 'cultivation limit' (Swedish *odlingsgränsen*, a juridical border created in the late 1800s to limit agricultural settlements in alpine areas designated to Sámi reindeer-herding practices; Lundmark, 2006; Axelsson, Angelstam & Svensson, 2007). South of the cultivation limit we connected year-round reindeer grazing areas to differentiate boreal forest and alpine areas (Fig 1). Moreover, our eastern and southern border for alpine areas corresponds to the limit of areas with persistent spring snow cover correlated with worldwide wolverine distribution (cf. fig. 3 in Copeland *et al.*, 2010; Supporting Information Figs S1 and S2). Thus, we used habitat, land-use practices, bioclimatic conditions and prey availability (i.e. year-round reindeer presence, the only medium-sized ungulate prey for wolverines) to delineate 'typical' wolverine habitat in alpine areas from lower-altitude boreal forest landscape. We performed all spatial analysis in ArcGIS 10.1 and maps were available from the Swedish Mapping, Cadastral and Land Registration Agency (www.lantmateriet.se).

Pilot study of monitoring methods

This part of the study was conducted in a 350-km^2 area in the southern part of Dalarna county (60°17′N 14°58′E) (Fig. 1) in 2013 and 2014. This area represents the extreme south of present wolverine occurrence, based on recorded observations (Fig. 2c) and reports from local residents who have observed wolverine tracks in the area during the last 6–8 winters (Aronsson & Persson, 2012). The habitat is mainly managed boreal forest (Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*), interspersed with mires, lakes and smaller settlements. Elevation ranges from 150 to 500 m a.s.l, and mean temperature ranges from −6°C (January) to 17°C (July). Average dates for first and last day with snow cover ≥5 cm are November 17 and March 31, respectively. Daily snow depth for the study period was accessed from the closest weather station (Dala-Järna, 60°32′N 14°21′E), northwest of the study area (available at: www.smhi.se). Potential food sources for wolverines in the study area are moose *Alces alces*, roe deer *Capreolus capreolus*, tetraonids, beaver *Castor fiber*, mountain hare *Lepus timidus* and rodents. Wolves *Canis lupus*, brown bears *Ursus arctos*, lynx *Lynx lynx* and red fox *Vulpes vulpes* occur in the area.

Together with local volunteers, we opportunistically searched the study area by car or ski when snow conditions were favourable to find wolverine tracks in the snow to mimic the official monitoring protocol implemented in northern areas. When tracks were found we followed them to search for suspected den sites using the established monitoring protocol and collect samples (scats, hair or anal gland secretion) for DNA analysis. All samples were genetically analysed within the national monitoring programme for sex and individual identity (see Wolverine monitoring and population estimates). In addition, from 15 February 2013 to 2015 January 2015 we used six camera stations (Fig. 1) within a 200-km^2 area in the centre of the study area, corresponding to the size of one female home range (Persson *et al.*, 2010). Camera stations were constructed following Magoun *et al.* (2011) and consisted of a run pole where wolverines are supposed to stand and reach for overhanging bait, showing abdominal and chest area to enable individual and sex identification. We used two motion-detecting infrared cameras (PC800; RECONYX Inc., Holmen, WI, USA) at each camera station, one for frontal pictures and one on the ground to document wolverines visiting the site without climbing the run pole. The cameras took one picture per second when an animal moved in front of it. Sites for camera stations were selected based on information from locals about frequent observations of wolverine tracks to maximize the chance to be visited by a wolverine (cf. Magoun *et al.*, 2011). We used parts of moose, roe deer and beaver obtained from road kills or from hunters as bait and visited all camera stations at least once every second month (range: 2–8 weeks) to retrieve photos, check battery status and change bait. We defined all wolverine photos taken within a maximum of 30 min as belonging to a single visit.

Results

Population trend

Since the start of the monitoring programme, a total of 1477 reproductions have been registered in Sweden, of these only 13 (<1%) were registered outside the reindeer husbandry area (Fig. 3a). At the start of the monitoring programme,

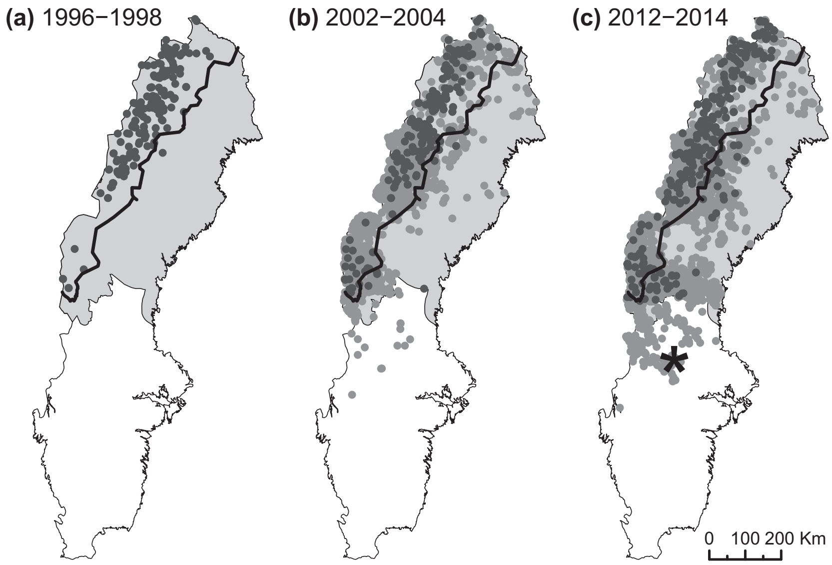

Figure 2 Wolverine population distribution trend in Sweden based on reproductions (black dots) and observations (grey dots) registered within the national monitoring programme. Monitoring results are presented for 3-year periods; (a) start of the monitoring programme, (b) wolverine observations started to be registered and (c) current distribution range of reproductions and observations. The star (*) shows the location of the pilot study. Shaded area shows the reindeer husbandry area and black line shows the border used to differentiate alpine areas and boreal forest landscape. Snow depth and days with persistent spring snow cover increase to the northwest (Supporting Information Figs S1 and S2).

reproductions were almost exclusively registered in alpine areas (Fig. 2a). Thereafter, both the number and distribution of reproductions in the forest landscape has increased (Fig. 2b and c), and since 2002 there has been at least one reproduction registered within the forest landscape each year, although mostly within the reindeer husbandry area (Fig. 3a).

Similar to the reproductions, the number and distribution of wolverine observations has increased in the boreal forest landscape (Fig. 2b and c) from 303 in 2004 to 643 observations in 2014 (Fig. 3b).

Based on observations registered within the monitoring programme in 2012–2014 the wolverine distribution in Sweden covers ~171 000 km^2, reaching ~170 km south of the reindeer husbandry area and ~190 km south of the southernmost registered reproduction. Furthermore, in 30% (52 100 km^2) of this range there has never been any reproduction registered, and 49% (25 700 km^2) of the area without reproductions is south of the reindeer husbandry area.

Pilot study of monitoring methods

In 2013–2014 we collected 32 scat samples for genetic analysis, of which 66% were successfully genotyped, and from these four individuals (one female and three males) were identified. Only one of the males had previously been documented in this area within the monitoring programme using DNA (one sample in 2008). From the camera stations we obtained 9784 photos in 3882 camera-days (Supporting Information Table S1 and S2). Wolverine was the most frequently photographed species (59% of photos) followed by red fox (10%) and pine marten *Martes martes* (8%), see Supporting Information Table S2 for a complete list of

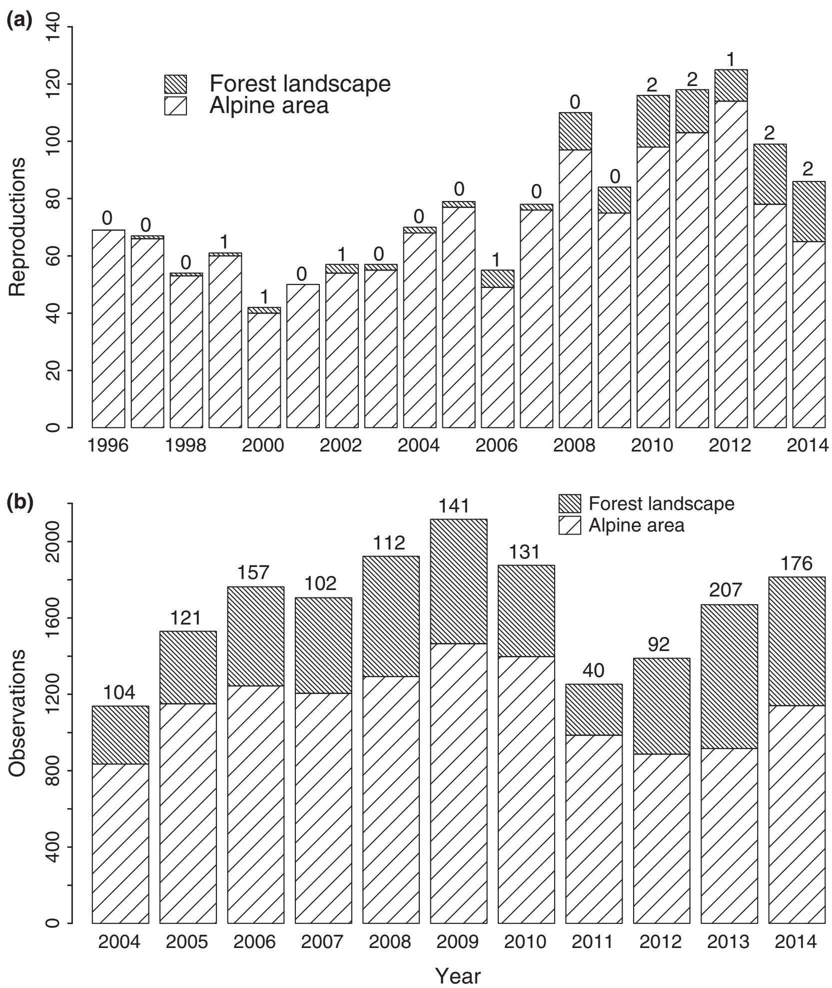

Figure 3 Number of wolverine reproductions (a) and observations (b) registered within the monitoring programme in Sweden each year (monitoring of reproductions started in 1996 and registrations of observations started in 2004). Shading of the bars shows the proportion of reproductions and observations located in alpine areas versus the boreal forest landscape. Numbers above bars represent reproductions and observations registered south of the reindeer husbandry area each year.

photographed species. In 16% of the photos there were no visible animals, presumably because moving branches or intense sunlight triggered the camera. Wolverines were photographed at all 6 camera stations during a total of 66 visits, of which wolverines were photographed on the run pole during 39 visits (59%). Time from set up of the camera station to first wolverine visit varied greatly among camera stations (mean ± SE: 92 ± 41 days) (Supporting Information Table S1). We identified five different wolverine individuals based on chest patterns; two males, one female and two of unknown sex. We identified the individual in 82% ($n = 32$) of the visits when the wolverine was photographed on the run pole, and identified the sex in 21% ($n = 8$) of the visits.

Discussion

Our assessment clearly shows that the Swedish wolverine population is expanding into the boreal forest landscape east and south of the alpine area, as well as outside both the reindeer husbandry area and areas with persistent spring snow cover. This implies that wolverines are now in the process of recolonizing what is believed to be their historical distribution (Persson & Brøseth, 2011), and that the political goal for the distribution of the species could be attained (SEPA 2014). We suggest several explanations for this range expansion. The wolverine population has increased considerably in alpine areas (Persson *et al.*, 2015), presumably leading to an increased number of dispersers colonizing forest landscapes. Moreover, from 1996 to 2015 the Scandinavian wolf population increased from 4 to 57 packs (Wabakken *et al.*, 2001; Anon, 2015*b*), and is now overlapping with most of the wolverine distribution south of the reindeer husbandry area. This has presumably increased year-round scavenging opportunities for wolverines on remains from wolf kills (van Dijk *et al.*, 2008). In addition, the annual moose hunt provides significant amounts of meat each autumn (Wikenros *et al.*, 2013) that can be cached and utilized for extended periods. These scavenging opportunities presumably facilitate wolverine establishment and reproduction (cf. Persson, 2005; Rauset, Low & Persson, 2015) south of the reindeer husbandry area, and thus buffer for potential negative effects of decreased snow cover. Hence, this expansion into areas without persistent spring snow cover suggests a less strict relationship between wolverine distribution and snow cover than previously hypothesized (cf. Copeland *et al.*, 2010). It remains unclear what will limit the southwards expansion of wolverines in Sweden, but we suggest that this limitation will be the result of interactions among availability of snow cover for denning and food caching (Copeland *et al.*, 2010; Inman *et al.*, 2012), competition from other predators and scavengers and food availability (Persson, 2005; Mattisson *et al.*, 2011; Rauset *et al.*, 2015).

While wolverines seem to cope better than expected with non-persistent spring snow cover in south-central Sweden, the monitoring protocol does not. Wolverine reproductions are only found in 70% of the wolverine range (as defined by recurrent wolverine observations). As population size estimates are based solely on reproductions, this strongly suggests that wolverines in about one-third of their range are not included in population size estimate. This is due to decreasing possibilities to fulfil the monitoring criteria for reproductions south and east of alpine areas, due to poor snow conditions at lower altitude and latitude (Anon, 2015*a*), as well as low monitoring effort. Consequently, there is a need for modification of the current monitoring programme to obtain relevant population estimates.

The current monitoring protocol was developed for northern alpine areas because it was only in those areas where wolverines were present at the onset of the monitoring programme in Scandinavia (Fig. 2). Our pilot study demonstrates a clear example of the need for survey methods that do not require persistent snow cover, as the snow cover was very poor for snow tracking shortly after wolverine females give birth and initiate denning (Fig. 4). The average date when a reproduction fulfilled the criteria to be registered as *documented* within the monitoring programme in 2013–2014 was April 17 ($n = 111$; Rovbase). Hence, it would have been exceptionally hard to document a reproduction in our study area following the current monitoring protocol (Fig. 4). Furthermore, to conduct a bare ground investigation of a suspected den site in early summer (see Supporting Information Appendix S1), the suspected den site has to be located by snow tracking during the spring. Considering that the average date for the first detection of suspected den sites in 2013 and 2014 was March 24 ($n = 180$; Rovbase) this alternative would also be hard to implement. However, using camera stations we documented the presence of at least five different individuals within a very limited part of the sampled area that is not supposed to contain wolverines according to national population estimates (Anon 2015*a*). The development of a camera-trapping protocol where camera stations specifically developed for wolverines are efficiently implemented over larger areas could provide a snow-independent method to record information on wolverine distribution, sex ratio, population density estimates (cf. Royle *et al.*, 2011) and most importantly the presence of resident females, which would help locate suspected den sites. Furthermore, because camera stations are suitable for identifying lactating females (Magoun *et al.*, 2011), they could be integrated as a snow-independent criterion for reproductions. As reproductions are the main unit for the conservation performance payment in Sweden, and the monitoring of reproductions provides indirect protection from poaching for wolverine females, and presence of reproductive females provides important information about population status (Persson *et al.*, 2015), it is important to continue using reproductions as the main monitoring unit. DNA collected from non-invasive samples can be used in retrospect to confirm reproductions (Flagstad *et al.*, 2004). However, DNA collection needs to be done in a less snow-dependent way than scat sampling, as wolverine scats are hard to find and to distinguish from other species without corresponding footprints in snow. One alternative is to collect DNA with hair snags at camera stations (cf. Magoun *et al.*, 2011).

Apart from the snow-dependent monitoring system, the southwards population expansion *per se* provides a challenge for wolverine management in Sweden. South of the reindeer husbandry area in Sweden there is no documentation of wolverine depredation on livestock (Frank, Månsson & Zetterberg, 2016), hence wolverines are subject to low levels of human conflict. Therefore, these areas may be of critical importance for wolverine conservation. However, management efforts south of the reindeer husbandry area are mainly focused on wolf and lynx as these are more controversial species in this area (Andrén *et al.*, 2006; Liberg *et al.*, 2012*b*). Thus, in the southern part of wolverine distribution monitoring is limited to opportunistic documentation of snow tracks and scats from wolverines registered during wolf or lynx monitoring (Fig. 2; Aronsson & Persson, 2012). For example, within our pilot study area we identified five and four different individuals using camera stations and DNA from scat samples, respectively, and even though locals have reported wolverine presence the past 8–10 years, only DNA from one individual had been sampled once in this area within the monitoring programme before our study. Furthermore, although wolverines are regularly observed over vast areas up to 170 km south of the reindeer husbandry area (Fig. 2), only 2 of 86 reproductions in 2014 were registered south of the reindeer husbandry area (2.3%, Fig. 3a) and there is no population estimate available for this part of wolverine range (Anon 2015*a*).

The consequence of the current situation is that wolverine management decisions in Sweden are not based on the status of the entire population. Such a scale mismatch may have impact on conservation outcomes when management actions cannot be adapted to national population goals (Linnell, 2015). This clearly shows that systematic monitoring of the entire population is needed to conduct adequate, population-level adaptive management in relation to national goals. The

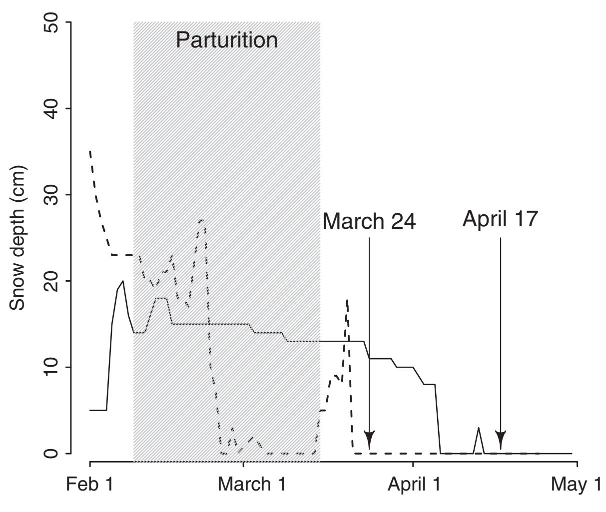

Figure 4 Daily snow depths during the spring for the pilot study area in 2013 (solid line) and 2014 (dashed line). Shaded area shows peak parturition period for wolverines (Inman *et al.*, 2012). Arrows show average dates for the first detection of suspected den sites (March 24) based on snow tracking and when reproduction fulfilled the criteria to be considered *documented* (April 17) within the monitoring programme in 2013 and 2014, based on snow tracking.

observed range expansion is an important step towards the political goal of increasing the wolverine range to reduce depredation levels within the reindeer husbandry area (SEPA, 2014). In particular, this highlights the need for implementation of snow-independent, flexible monitoring techniques adapted to local conditions. Lethal control is currently the main management tool to decrease predation by wolverines because few preventive measures are applicable to modern, extensive reindeer herding (Persson *et al.*, 2009). However, harvest rates need to balance conflict mitigation, attainment of favourable conservation status (Council of the European Union, 1992) and national population goals. Consequently, it is important that harvest rates are set in relation to the total population size. The scale mismatch where official population estimates do not reflect reality may hinder conflict mitigation within the reindeer husbandry area, that is, the room for implementation of lethal control in high-conflict areas is influenced by the number of wolverines outside the reindeer husbandry area. If conflict mitigation is limited by known underestimation of population size, this could have detrimental consequences for stakeholders' trust in management (Young *et al.*, 2016), and thus decrease acceptance for wolverines and their conservation in the reindeer husbandry area.

In summary, we have illustrated how Swedish wolverine management neglects changing conditions by only focusing on high-conflict areas, and thereby misses an opportunity to adequately evaluate management goals and to efficiently manage human–carnivore conflicts for long-term carnivore conservation. This provides an important example of how carnivore management often concentrate actions to specific parts of populations, commonly in protected areas or high-conflict areas (Linnell, Swenson & Andersen, 2001; Balme *et al.*, 2013). Instead, the key to successful carnivore conservation requires flexible management policy adapted to biologically relevant scales and to ecological change, and thus considers the entire range of conditions under which carnivores, the environment and people interact because the solution may be found outside areas with high management focus.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Mean number of days per year with snow cover in Sweden from the measurement period 1961–1990.

Figure S2. Mean snow depth and proportion of years with snow cover in Sweden on the 15th of March from the measurement period 1961–1990.

Table S1. Information for each camera station regarding period activated, total number of wolverine visits and time from deployment to first wolverine visit.

Table S2. Complete list of mammal and bird species photographed at camera stations, total number of photos and number of visits for each species.

Appendix S1. Description of monitoring criteria for a wolverine reproduction to be classified as *considered certain* within the Scandinavian monitoring programme.