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LETTER

Paying for an Endangered Predator Leads to Population Recovery

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Abstract

Keeping viable predator populations on a human-dominated planet will require innovative approaches that promote local coexistence with human activities. Conservation performance payments, which are linked specifically to the production of a desired environmental output, have received increasing attention but their effectiveness in predator conservation remains undocumented. Here, we show that paying Sámi reindeer herders for wolverine (*Gulo gulo*) reproductions has been instrumental in the recovery of wolverines in Sweden. Adult female wolverines were significantly less exposed to illegal killing and this allowed the population to more than double in a decade. We argue that this program provides protection for adult female wolverines through a combination of direct monetary value and indirect protection because of monitoring activities. The program's success, even in a system where livestock is the main prey for the predator, reveals an exceptional potential for future implementations in large carnivore conservation.

Introduction

The conflict between carnivore conservation and reducing the negative effects of carnivores on local communities raises a need for innovative methods to promote human-carnivore coexistence (Dickman *et al.* 2011; Hobbs *et al.* 2012; Chapron *et al.* 2014; Ripple *et al.* 2014). To date, conservation strategies of large carnivores have generally relied on two principal approaches: (1) benefit from legal protection in many countries (Trouwborst 2010) and (2) prevention and compensation for depredation to support livestock farmers negatively affected by carnivores (Wagner *et al.* 1997; Naughton-Treves *et al.* 2003; Schwerdtner & Gruber 2007; Maclennan *et al.* 2009). However, both approaches have inherent limitations because they do not provide incentives for human-carnivore coexistence. Despite strict protection laws, illegal killing is one of the most important mortality sources for large carnivores (Andrén *et al.* 2006; Chapron *et al.* 2008; Liberg *et al.* 2011) and compensation systems are often associated with a perverse incentive (e.g., reduced incentives to protect livestock), limiting their conservation impact (Nyhus *et al.* 2003; Zabel *et al.* 2011).

Because of these limitations, there has been increasing interest in alternative approaches to promote carnivore-human coexistence (Nelson 2009; Dickman *et al.* 2011; Treves & Bruskotter 2014), such as giving carnivores a direct nonconsumptive value through conservation performance payments (CPP). CPP establishes a direct link between monetary payments and the production of desired conservation objectives (Ferraro 2001; Ferraro & Kiss 2002; Engel *et al.* 2008; Nelson 2009; Zabel & Roe 2009; Zabel & Engel 2010; Dickman *et al.* 2011). Thus, CPPs differ from general subsidies (that are not linked to achievements) and compensation schemes (linked to level of damages; Zabel and Roe 2009). However, there has never been a rigorous evaluation of the effectiveness of CPPs to promote coexistence between people and predators. This lack of evaluation has precluded a widespread adoption of CPP programs (Nelson 2009) despite the potential benefit to both carnivores and local human communities.

To date, the most well-established population-wide and publicly funded CPP program targets wolverines (*Gulo gulo*) and other large carnivores in the Swedish reindeer husbandry area (Zabel & Holm-Muller 2008).

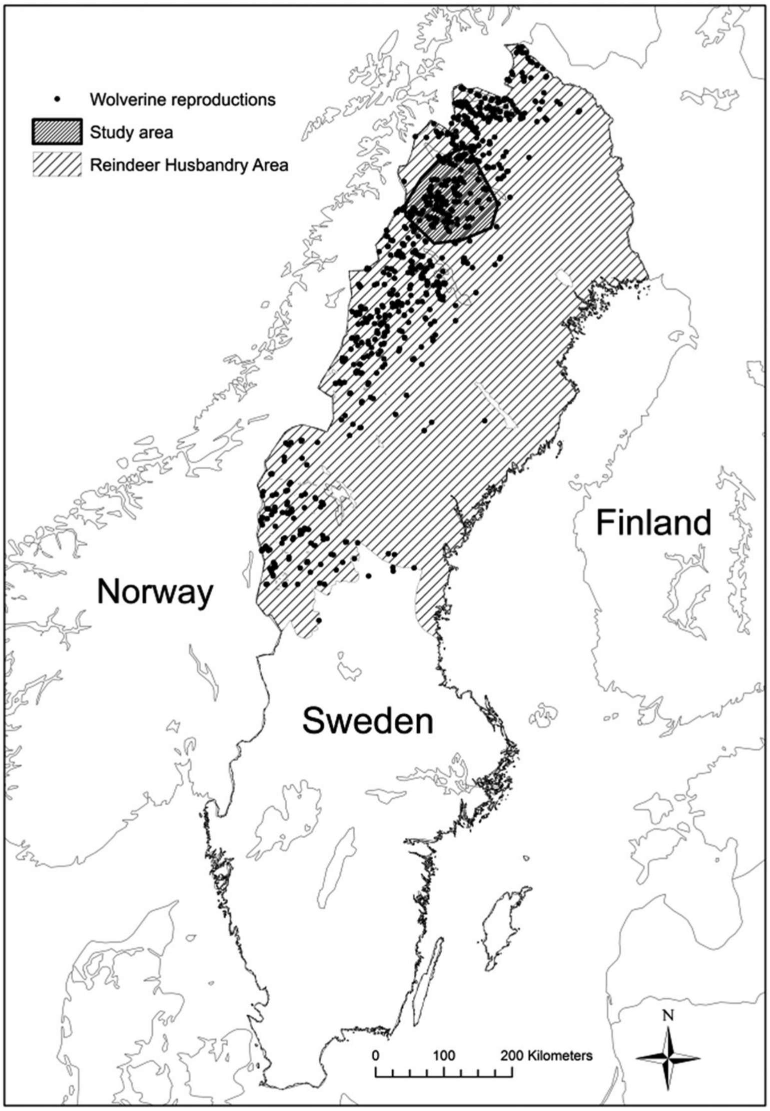

Figure 1 Map of the study area (black border) with dots showing recorded wolverine reproductions (1996–2012) and shading showing the reindeer husbandry area.

The wolverine is a protected species in Sweden and its distribution is mainly restricted to the reindeer husbandry area (Figure 1) where they are largely dependent on semidomestic reindeer (*Rangifer tarandus*) for prey, with few alternative food sources available. Semidomestic reindeer are owned and herded by indigenous Sámi people, and because reindeer graze freely over extensive areas, it is difficult to implement efficient preventive measures against depredation. One consequence is illegal killing, which is the most important source of adult mortality in Swedish wolverines (Persson *et al*. 2009). Depredation by wolverines on semidomestic reindeer creates conflicts between carnivore conservation and the sustainability of an indigenous culture (Hobbs *et al*. 2012). Thus, the wolverine-reindeer system represents an extreme case of predator-livestock coexistence and an exceptional conservation challenge.

In 1996, Swedish authorities changed from a compensation system to a CPP program that offset reindeer depredation losses and created incentives for wolverine conservation. In this program, authorities make payments to reindeer herders based on the number of documented wolverine reproductions in their districts (Landa *et al*. 1998), regardless of predation levels (Zabel & Holm-Muller 2008). Thus, an integral part of the CPP program is an extensive system for monitoring wolverine reproductions in the field (i.e., snow tracking in March-May to identify natal dens and/or observe females with cubs (Landa *et al*. 1998)). Payments are intended to cover losses in reindeer production resulting from depredation or disturbance, while simultaneously accounting for the conservation value of wolverines (Statens Offentliga Utredningar 2007). From 1996 to 2001, payment was based on a set total amount for losses to wolverines (and lynx) in the reindeer husbandry area, divided by the number of reproductions per species; in practice, this meant the payment per wolverine reproduction was lower than the originally intended 200,000 SEK (SEK 1 ≈ €0.15). Since 2002, payments have been set at 200,000 SEK per documented wolverine reproduction, with ~18 million SEK paid annually. To assess whether there is evidence that this CPP has had a positive demographic effect on its performance indicator – i.e., the annual number of reproducing adult female wolverines – we used long-term data from radio-marked adult resident wolverines and data from the national population monitoring program.

Methods

We used individual-based demographic data from radio-marked wolverines from an area in northern Sweden (18°E 67°N) from 1996 to 2011 (Persson 2005; Persson *et al.* 2009). This area includes important spring–autumn grazing pastures for semidomestic reindeer, but some reindeer remain during the winter season. Data were from 95 (>2-year-old) wolverines (33 males; 62 females) monitored during 356 radio years (Persson *et al.* 2009), and used to estimate cause-specific mortality rates for adult males and females (Heisey & Patterson 2006) in R (Sargeant 2011; R Core Team 2014). For population model parameterization (see below), we used the same method to estimate age-specific mortality rates for 234 wolverines (163 monitored as juveniles, 106 as subadults, and 95 as adults). We also estimated reproductive rates for 62 females during 251 potential reproductive events.

We estimated the effect on population growth rate of illegal killing of females using a two-sex stochastic individual-based population model, with a three-stage population structure: resident sexually mature adult individuals (>2-year-old), subadults/floaters (1–2-year-old), and juveniles (<1-year-old). Resident sexually mature individuals are male or female territory holders with the possibility of reproducing each year. Floaters and juveniles are nonresident, nonreproducing individuals. Wolverines exhibit a polygamous mating system, where one male overlaps and mates with several females each year (Hedmark *et al.* 2007). We modeled the wolverine polygamous mating system by calculating the probability P of an individual female reproducing as $p = \max(\frac{\alpha \cdot N_m}{N_f}, 1)$ where $\alpha = 4.38$ is the average number of breeding females per breeding male, N_m is the number of sexually mature resident males and N_f is the number of sexually mature resident females.

We parameterized our model for adult survival with rates estimated above. We considered that reproduction takes place from age 2 to age 13, with average number of female cubs per 2-year-old female $f_2 = 0.05$ and per year, and average number of female cubs per sexually mature female and per year $f = 0.38 \pm 0.04$. We assumed that the wolverine population in Sweden is well below its carrying capacity and that density-dependent effects are negligible compared with other factors affecting mortality and reproduction. We ran Monte Carlo simulations (1,000 runs per parameter set) to investigate how different levels of illegal killing on males and females would affect population growth rate.

To estimate if a difference in illegal killing rates between males and females could be due to one sex being easier to kill than the other, we used wolverine harvest data in Norway as a control (i.e., the same population as in Sweden but where wolverines are legally hunted; data from 1995 to 2012, $n = 709$; accessed from Rovbase 3.0). We separated harvest methods into trapping (by box traps), license hunts (most animals shot with rifle at bait sites or during hunting for other game), and lethal control by management authorities.

Results

Adult females had an average (±SE) annual risk of being illegally killed (0.08 ± 0.02) that was significantly lower ($\chi^2 = 4.71$, df = 1, $P = 0.03$) than the average (±SE) risk for adult males (0.21 ± 0.06). In contrast, there was no evidence of a difference for annual natural mortality risk for females (0.07 ± 0.02) versus males (0.03 ± 0.03) ($\chi^2 = 1.27$, df = 1, $P = 0.26$). Based on the Norwegian harvest data, there was no evidence that the higher risk for males of being illegally killed was a consequence of biological factors increasing their risk: the harvest proportion for males was 50% and was not affected by harvest type (44% of trapped [n = 34] and 49% of shot [n = 373] during license hunt, and 51% for government lethal control [n = 302]). Similarly, North American data (Krebs *et al.* 2004) did not reveal any difference in male and female survival in trapped populations, suggesting that male and female wolverines are equally vulnerable to human killing. The lower risk of illegal killing for females contributed to an observed positive growth rate of the population ($\lambda = 1.04 \pm 0.25$) since 1996 inside the reindeer husbandry area. Similarly, growth rate calculated from a wolverine-specific individual-based model was $\lambda = 1.06 \pm 0.02$ with the observed male and female illegal mortality rates included; however, if illegal mortality risk

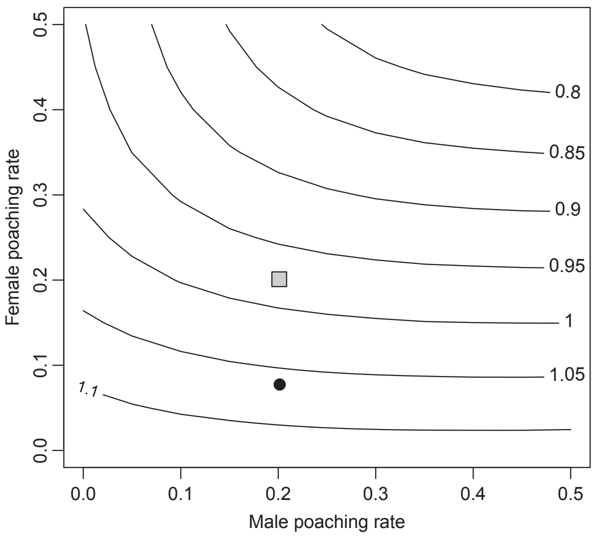

Figure 2 Population growth rate contour curves as a function of male and female illegal killing rates, highlighting its sensitivity to female poaching. The black circle indicates actual illegal killing rates for the Swedish wolverine population (females = 0.08; males = 0.21); the gray square is if illegal killing of females was the same as males. Other demographic parameters do not vary and are based on the Swedish wolverine population.

for females was assumed equal to that for males, the estimated population growth rate was negative ($\lambda = 0.97 \pm 0.02$; Figure 2).

Discussion

The population history of Swedish wolverines is consistent with changes in national management policy. After the introduction of strict legal protection and penalties against illegal killing in 1969, the population decline began to reverse but this recovery was extremely slow during the next 27 years (Statens Offentliga Utredningar 2007). When the CPP program became fully operational in 2002, the number of registered reproductions was 57 (Landa *et al.* 1998). By 2012, the number of registered reproductions had increased to 125, with the population expanding into previously unoccupied areas (Viltskadecenter 2012). This growth rate is remarkable given the fact that Swedish wolverines are part of a larger population shared with Norway, which annually harvests ~14% of their population (data accessed from Rovbase 3.0). The Norwegian part of the population presumably represents a sink that is sustained by the Swedish part of the population, and this may explain why the population did not grow as much as our model predicted.

Although our study cannot accommodate a before-after longitudinal treatment because data before 1996 are of poorer quality, we can use additional evidence for the CPP effect by comparing Sweden with Finland. Northern Sweden and Finland share the same socioecological context with extensive reindeer herding. However, Finland has not implemented a CPP with wolverine conservation relying exclusively on strict protection laws and compensation for damages to reindeer (Kaczensky *et al.* 2013). Finnish monitoring data show that there are extremely few reported wolverine reproductions within the Finnish reindeer husbandry area (Wikman 2010; Kaczensky *et al.* 2013), with the implementation of protection and compensation system not appreciably increasing population growth.

In our study, no changes in Swedish wolverine population growth were observed until 5 years after the adoption of the CPP. We propose three nonmutually exclusive factors to explain this: an institutional lag (the CPP program was not fully financially implemented until 2002), a social lag (it took time for the new system to be understood and accepted), and an ecological lag (wolverine females have a low reproductive rate and reproduce the first time when they are 3–5 years old (Persson *et al.* 2006)).

The CPP appears to provide protection for wolverine females in Sweden through a combination of structural, spatial, and temporal mechanisms. Because reproducing females are the indicator for the program, they de facto have a monetary value and are thus expected to constitute a segment of the population that poachers will deliberately avoid. Another important mechanism is that monitoring activity is inherently spatially concentrated around denning habitat and potential den sites during the denning period. Therefore, poachers are likely to avoid these areas; indeed, no poaching attempts at den sites have been reported since 1996, while digging out dens to kill females with offspring occurred frequently before. As monitoring takes place in March–May when illegal killing is facilitated by beneficial snow and light conditions (Persson *et al.* 2009) it also acts as a temporal deterrent against illegal killing. Overall, this program creates a strong negative incentive toward illegal killing in the neighborhood of known denning sites. Thus, the CPP can be seen as a case of situational crime prevention that reduces opportunities for a specific category of crime by increasing associated risks and reducing the reward (Clarke 1995).

In addition, since County Administration staff conduct the monitoring in collaboration with reindeer herders, a spillover effect of the program may be an increased acceptance for both wolverines and the management as regular communication and interaction between representatives of "the buyer and the seller" (Zabel & Engel 2010) can improve trust and understanding. However, because our analysis did not allow us to disentangle the indirect protective effect of monitoring from the direct effect of monetary value, it is unclear how this program would perform if monitoring would not require an extensive presence in the field around den sites.

Conclusion

Our study highlights the importance of choosing the most efficient indicator when a CPP program is implemented. In our case, the program was successful in promoting wolverine recovery because the indicator was chosen to be the demographic segment to which population growth is the most sensitive (i.e., reproductive females; Figure 2). Therefore, a key to the success of CPP is to attain a match between what is rewarded and what is desired to generate the right incentives. In addition, because payment is made regardless of actual losses, efficient herding (to prevent depredation) is economically beneficial and not penalized by lower compensation. Importantly, because the Swedish CPP program focuses on an extreme case, where a large carnivore feeds mainly on livestock, its success illustrates a very promising potential for future implementation in carnivore conservation, especially where livestock is not the main prey.

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