

Swan View Coalition

Nature and Human Nature on the Same Path



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September 29, 2016

Flathead National Forest
Attention: Forest Plan Revision
650 Wolfpack Way
Kalispell, MT 59901

Re: Research Papers on Ecological Traps and Dispersing Grizzly Bears
Submitted via <https://cara.ecosystem-management.org/Public/CommentInput?Project=46286>

Dear Folks;

We've attached four research papers and reference a fifth that you should have in the planning records. These papers deal with the movement of grizzly bears into previously occupied habitats, including movement into areas now heavily occupied by humans and their developments, resulting in what is known as "ecological traps." All of these papers to some degree call into question the prevailing attitude on the part of the Forest Service and Fish and Wildlife Service that the NCDE grizzly bear population has recovered, is increasing steadily at over 2% per year, is expanding its range due to population pressures, and should have its protections under the ESA removed.

We will discuss briefly each of these papers and urge that the agencies adopt a more conservative approach to grizzly bear recovery. It is high time to recognize the increasing negative effects human developments are having on grizzly bear, to carry forward and finish implementing Amendment 19, to extend A19 protections to other areas needed for population expansion and dispersal, and to recognize DEIS Alternative C as the preferred alternative and not regard it solely as an outlier or benchmark.

We also incorporate by reference the comments submitted by Friends of the Wild Swan today and, in turn, the comments submitted by Montana Ecosystems Defense Council.

Lamb et al. 2016 - "Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore."

This paper describes the phenomena of an "ecological trap" in Canada resulting from grizzly bears putting themselves at significant risk to pursue berries in an area of high human density.

. . . an ecological trap (ET) can occur when an animal is presented with novel conditions and the animal's assessment of habitat quality is poorly matched to its resulting fitness . . . Our results demonstrate that a valley high in both berry resources and human density was more attractive than surrounding areas, and bears occupying this region faced 17% lower apparent survival. Despite lower fitness, we detected a net flow of bears into the ET, which contributed to a study-wide population decline.

Hale et al. 2015. "Evaluating the metapopulation consequences of ecological traps."

This paper looks more broadly at ecological traps and concludes:

Ecological traps are likely to become increasingly common as humans continue to dramatically alter the landscape . . . Incorporating traps into management and conservation practices will require close tracking of changes both in 'real' and perceived habitat quality over time, and a greater consideration of animal behavior.

Mowat and Lamb 2016. "Population status of the South Rockies and Flathead grizzly bear populations in British Columbia, 2006-2014."

This paper contends with short-term population declines and recovery in southern B.C., Canada:

The grizzly bear population north of Highway 3 . . . declined about 40% between 2006 and 2013 . . . South of Highway 3, in the Flathead valley, the population declined between 2007 and 2010 and increased from 2010 to 2014 . . . which suggests the decline McLellan (2015) observed was geographically broader than his study area . . . the population decline . . . was probably precipitated by a decade of poor forage production which occurred during a series of summers that were unusually dry compared to the previous two decades.

Mikle et al. 2016. "Demographic mechanisms underpinning genetic assimilation of remnant groups of a large carnivore."

This paper uses DNA parentage analysis from 2004 - 2012 to examine the influence of dispersing grizzly bears on genetic diversity in portions of the NCDE:

Despite the significant increase in genetic diversity, nearly all (37/45 - 82%) of the southernmost females detected in the SE periphery descended from three females, illustrating a trend that is likely to continue at the expansion front due to male-biased dispersal of grizzly bears . . . Edge populations may be particularly important sources of genetic diversity that may enable species persistence particularly in changing environments . . . Numerous populations of

carnivores persist as remnants, largely due to habitat fragmentation and persecution, with climate change expected to exacerbate the problem . . . Patterns of genetic diversity in populations are dynamic in space and time, particularly for species undergoing changes in population dynamics and geographical distributions. Extreme changes can occur in less than a single generation and are surprisingly idiosyncratic and stochastic . . . As such, we suggest caution when making landscape-scale conservation and management decisions based on a single sampling snapshot in time.

In other words, the current dynamics in the NCDE and its Canadian counterpart cannot be explained as simply as the DEISs and FWS would like to. It is dangerous and wrong to describe the NCDE population as recovered and increasing steadily at over 2% per year, multiplying Kendall's 2004 population estimate by that percentage to claim there are some 1,000 grizzly bears today. It is equally dangerous and wrong to claim or imply that the dispersal of bears outside the initial recovery zone is a sign that the population is so robust that bears are being pushed out of their habitat by other bears.

Indeed, Mace and Waller's 199 "Demography and population trend of grizzly bears in the Swan Mountains, Montana" (Conservation Biology Vol.2, No. 5, Oct. 1998) found the population there to be declining 2.3% per year. Moreover, they found:

Our mortality, movement, and occupancy data suggest that the multiple-use zone is a population source area, and that wilderness and rural zones are sink areas . . . We recommend . . . protecting core areas on public lands of superior habitat through access management . . .

This source-sink dynamic found by Mace and Waller is not unlike the ecological trap phenomena documented by Lamb and others, with bears moving off the Swan Crest to seek lower elevation foods in often hostile and lethal habitats in the Swan Valley.

Researchers never have provide an explanation for continued demographic problems in the wilderness, leaving one to ponder whether the population there is still suffering from being hunted up until 1991, is still suffering from "shoot, shovel and shut up" mortality associated with big game hunting and other recreation, or is simply afforded drier and less productive habitats there. The agencies don't appear to want to describe how ecological traps and source-sink population dynamics fit into their rosy picture of a recovered and thriving NCDE bear population.

The above research calls into question the very conclusions and methods upon which "recovery" and "range expansion" are being based. Nowhere do the DEISs and FWS give serious consideration to alternative explanations of why grizzly bears may disperse into hostile territory to meet their nutritional needs, with greatly increased risks of mortality. Nowhere do the DEISs or FWS propose substantial habitat and bear protection measures to truly allow bears to disperse, take up residence, and link the NCDE with other ecosystems - rather than more likely simply ending up dead in ecological traps.

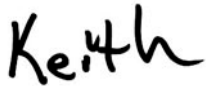
Nor have the DEISs or FWS ever measured NCDE habitat quality, quantity and security against “habitat-based recovery criteria” before claiming the population recovered. Nor, as explained in our 9/8/16 comment letter, do the DEISs or FWS provide habitat management standards that would either truly maintain 2011 levels of habitat conditions or continue to improve upon them as promised in existing Forest Plans.

We ask that you give serious consideration to this letter and the attached research papers. We ask that you err on the safe side in the face of climate change and increasing human impacts to bears and their habitat. We urge you to look to the future, recognize the conservation legacy the Flathead should and must provide, revise Alt. C to include A19, and make it your preferred alternative.

As you wrote of Alt. C on page 27 of DEIS Vol. 1, "this alternative would provide the highest habitat security and connectivity for species that may be sensitive to higher levels of human disturbance." It will provide even more by also providing the habitat security and connectivity promised under A19.

Thank you for this opportunity to comment.

Sincerely,

A handwritten signature in black ink that reads "Keith". The letters are cursive and slightly slanted to the right.

Keith J. Hammer
Chair

Attachments:

1. Lamb et al. 2016
2. Hale et al. 2015.
3. Mowat and Lamb 2016.
4. Mickle et al. 2016.

Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore

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Summary

1. Habitat choice is an evolutionary product of animals experiencing increased fitness when preferentially occupying high-quality habitat. However, an ecological trap (ET) can occur when an animal is presented with novel conditions and the animal's assessment of habitat quality is poorly matched to its resulting fitness.

2. We tested for an ET for grizzly (brown) bears using demographic and movement data collected in an area with rich food resources and concentrated human settlement.

3. We derived measures of habitat attractiveness from occurrence models of bear food resources and estimated demographic parameters using DNA mark-recapture information collected over 8 years (2006–2013). We then paired this information with grizzly bear mortality records to investigate kill and movement rates.

4. Our results demonstrate that a valley high in both berry resources and human density was more attractive than surrounding areas, and bears occupying this region faced 17% lower apparent survival. Despite lower fitness, we detected a net flow of bears into the ET, which contributed to a study-wide population decline.

5. This work highlights the presence and pervasiveness of an ET for an apex omnivore that lacks the evolutionary cues, under human-induced rapid ecological change, to assess trade-offs between food resources and human-caused mortality, which results in maladaptive habitat selection.

Key-words: apex species, attractive sink, bear, capture–recapture, compensatory immigration hypothesis, huckleberry, maladaptive habitat selection, mark–recapture, population growth, *Ursus arctos*

Introduction

Animals tend to use a series of cues established over evolutionary time to select habitats that maximize their fitness (Darwin 1859; Fretwell & Lucas 1970). However, maladaptive habitat selection can occur when novel conditions decouple the link between habitat quality and fitness, resulting in an ecological trap (referred to as ET hereafter; Dwyer & Boag 1972). ETs and human activity are often associated because human alteration of

the landscape tends to occur more rapidly than cues evolve to guide an animal's response to landscape changes (Robertson, Rehage & Sih 2013; Hale & Swearer 2015).

For an ET to exist, (i) individuals must show equal or greater selection for trap habitat relative to surrounding source habitats, (ii) the fitness of individuals using trap habitat must be lower than the fitness of individuals not using the trap, and (iii) to have persistent, population-level effects, animals must move from source habitats into the ET (Robertson & Hutto 2006; Runge, Runge & Nichols 2006; Hale & Swearer 2015; Hale, Treml & Swearer 2015). Although ETs have been reported in a number of studies (Hale & Swearer 2015), few cases meet all of the above criteria, and we know of no

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examples in large mammals. For example, Balme, Slotow & Hunter (2010) and van der Meer *et al.* (2013) highlight source–sink dynamics for African carnivores across the landscape but do not link this dynamic to truly attractive habitat, the key tenet of an ET. Similarly, Nielsen, Stenhouse & Boyce (2006) and Northrup, Stenhouse & Boyce (2012) provide evidence of grizzly bear selection of habitats associated with high mortality, but do not assess if this results in lower fitness or source–sink dynamics.

Apex consumers are highly vulnerable to ETs because they typically lack natural predators (Ripple *et al.* 2014) and may not perceive or avoid novel sources of risk such as human predation (Robertson, Rehage & Sih 2013). Consequently, conflicts with humans for space have resulted in severe range reductions for apex consumers globally (Morrison *et al.* 2007; Ripple *et al.* 2014; see grizzly bear example in Fig. 1). Conflict with humans is a ubiquitous concern for species in the *Ursidae* family, and the main drivers of conflict are anthropogenic food sources and expansion of human settlement (Can *et al.* 2014). Here we provide evidence for an ET for a wide-ranging, apex omnivore, the grizzly (brown) bear (*Ursus arctos*). Grizzly bears have high nutritional demands in preparation for hibernation (McLellan 2011; Lopez-Alfaro *et al.* 2013); therefore, areas with both attractive

food resources (natural or anthropogenic) and a high risk of human conflict could produce an ET for grizzly bears. At a fine scale, this mechanism is shown in grizzly bear selection for roads. In areas where road density is high, human–bear conflicts increase and grizzly bear fitness is severely reduced (Boulanger & Stenhouse 2014). However, bears do not consistently avoid roads and often select for spring forage along roadsides (Nielsen *et al.* 2002), which highlights a potential mismatch between perceived habitat quality and realized fitness benefits.

Grizzly bears in the Rocky Mountains select habitats with fruit resources (Nielsen *et al.* 2003, 2010), which increase fitness in the absence of human settlement (McLellan 2015). Our study focused on a region with abundant fruit resources for bears and locally concentrated human settlement. Human-caused mortality is the primary cause of death for grizzly bears, particularly in the southern portion of their range (McLellan, Hovey & Mace 1999), due to both hunting and non-hunting sources of mortality [e.g. conflicts with humans, road and railway strikes and poaching (Mowat & Lamb 2016)]. Consequently, we predicted an ET in our study area where abundant fruit resources and human settlement co-occur.

We tested the hypothesis that an area with intensive human development and rich food resources would

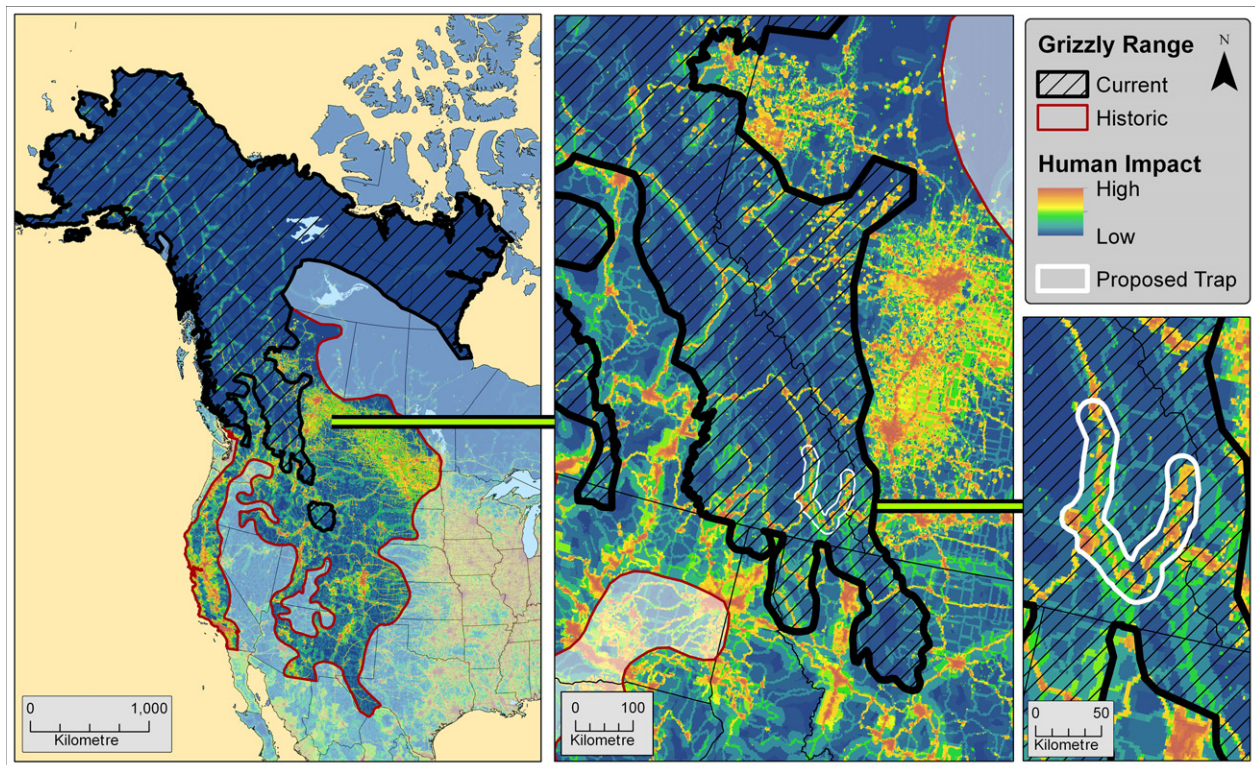


Fig. 1. Current and historical distribution of grizzly bears across North America (left) with Human Influence Index shown from high to low influence (HII, Wildlife Conservation Society – WCS, and Center for International Earth Science Information Network – CIESIN – Columbia University 2005). Middle: The eastern range margin of grizzly bears, showing the ‘cookie cutter’ grizzly bear range reduction resulting from human influence. Right: Proposed ecological trap area in south-east British Columbia, an area of both concentrated human settlement and rich bear habitat. Current distribution from most up-to-date local distributions from COSEWIC (2012), MFLNRO (2012), Rovang (2013), and historical distribution from Mattson & Merrill (2002) and COSEWIC (2012).

produce fitness consequences for a population of grizzly bears because of decreased survival in the trap and net immigration into the trap from adjacent source populations. We determined whether (i) the trap habitat was of equal or greater attractiveness than surrounding habitats; (ii) survival and/or reproduction in the trap habitat were reduced and insufficient to meet replacement; and (iii) bears from more remote areas moved into the trap habitat. Satisfying all three conditions would provide strong evidence for the presence of an ET.

Materials and methods

STUDY AREA

The study area covers 10 600 km² of the Canadian Rocky Mountains in south-eastern British Columbia (BC; Fig. 2). The region is bounded by the continental divide (BC–Alberta border) to the east, the Canada–United States border to the south, the Kootenay River, Rocky Mountain Trench and Wigwam River to the west, and the Palliser River to the north.

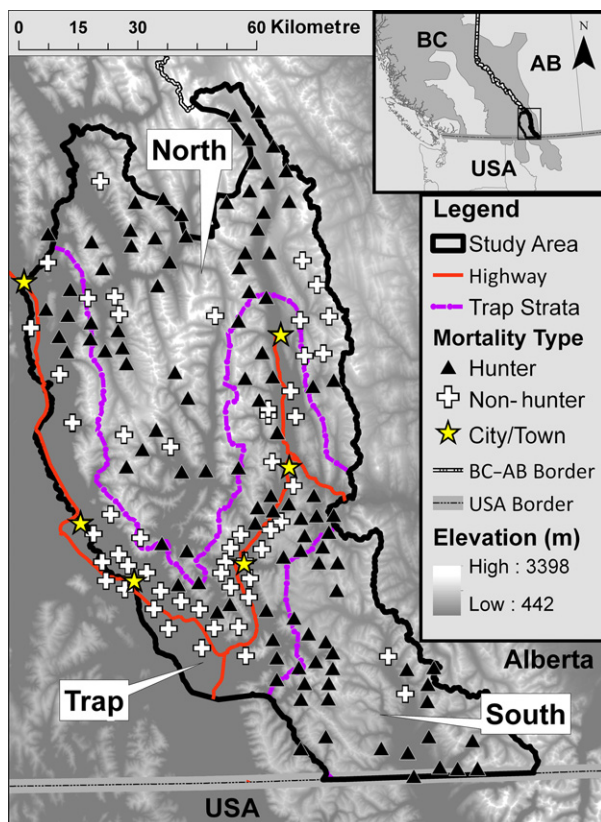


Fig. 2. Study area for the South Rockies Grizzly Bear Project, and locations of all recorded human-caused grizzly bear mortalities between 2006 and 2014 in south-east British Columbia, Canada. The Trap stratum buffers the highway (red line) and is shown as the polygon enclosed by the thick purple broken line. The recorded human-caused grizzly bear mortalities from 2006 to 2014 are shown by hunter (black triangle) and non-hunter (white cross) symbols. Towns are shown as yellow stars. Grizzly distribution in North America is shown in dark grey on the inset map.

There are approximately 12 000 people (Canadian population census 2006, 2011) residing in the area year-round, with a major influx of tourists during the summer months. The majority of human settlement occurs in the valley bottoms bordering the Elk and Kootenay rivers. Many highways intersect or border the region (Hwy 3, 43, 93, and 95), with high traffic volume during the summer months (>18 000 vehicles per day; BC Ministry of Transport). A railroad (Canadian Pacific Railway) follows the highway from Cranbrook to Elkford and continues to Alberta via Crowsnest Pass. The study area has abundant grizzly food resources, which are responsible for local bear densities exceeding 77 bears/1000 km² in the 1980s (McLellan 1989); the highest recorded interior grizzly densities in North America. Currently, bear density across the region is high and female skewed [F : 28 (± 6.8) and M : 15 (± 2.7)/1000 km²; Mowat *et al.* 2013].

To assess the potential for an ET, we divided the study area into three strata based on known concentrations of bear mortalities and human habitation in the region (Fig. 2). An ET stratum (hereafter referred to as the Trap) was created by buffering settled areas and highways by the average radius of a grizzly male home range in the region (11.2 km, Apps *et al.* 2004), amended to local topography (Fig. 2). Because grizzly female home ranges are smaller than those of males (Apps *et al.* 2004; Graham & Stenhouse 2014), both male and female bears residing outside the Trap buffer should have home ranges that generally do not overlap the highway, or have relatively little interaction with the highway and associated settled areas, the main area of reported grizzly bear mortality in this region (Fig. 2). We used relocations from collared grizzly bears in the Trap stratum to ensure our buffer encompassed the collared bears residing in the area (Apps *et al.* 2007). The remaining two strata consisted of the regions to the north and south of the Trap stratum, to the bounds of the study area, hereafter referred to as North and South, respectively (Fig. 2). For each stratum, we summarized the habitat attractiveness, local demography and movements between neighbouring strata.

HABITAT ATTRACTIVENESS

Black huckleberry (*Vaccinium membranaceum*, generally ripe between August 1 and September 15) and Canada buffaloberry (*Shepherdia canadensis*, generally ripe between July 1 and August 15) are attractive to grizzly bears (McLellan & Hovey 2001a; Nielsen *et al.* 2003, 2010), and consuming these high-energy foods confers fitness benefits in the absence of humans (Welch *et al.* 1997; McLellan 2011, 2015). As a result, we used the occurrence of these two species across the landscape to provide a representative measure of habitat attractiveness for grizzly bears. We built occurrence models for both fruiting shrub species using multivariate logistic regression and occurrence records from 1779 vegetation plots (20 × 20 m) conducted within the study area. Plots were stratified by biogeoclimatic features to ensure representation of widely differing ecological conditions. Using these data, we modelled berry species occurrence as a function of environmental variables hypothesized to predict occurrence, including climate, soil, topographic and fire variables (see Appendix S1, Supporting Information). We built models and occurrence maps and derived stratum-specific predictions of fruit occurrence using program R (R Core Team 2016). Occurrence records for each species were randomly divided into training (85%) and testing (15%) groups for model development and validation, respectively (Nielsen *et al.* 2005). We fit each of the eight models to the data and tested the

fit of the data to the model using Akaike's Information Criterion (AIC, Akaike 1974). The model with the lowest AIC score was considered the most parsimonious model, which we retained as our top model. The training data were used to assess the predictability of the top model using receiver operating characteristic (ROC) and the area under the curve (AUC) (Fawcett 2006) statistics.

We quantified a *per-capita* landscape occurrence of each fruiting species by dividing the total area of predicted fruit occurrence within each stratum by the abundance of bears occupying the stratum. We used this measure as an index to portray the availability and attractiveness of fruit resources in each strata, as the absolute area of fruit occurrence realized by a grizzly bear will depend on the degree of home range overlap and the per cent cover of each species within the occupied cells. Nevertheless, we believe this index accurately represents the relative *per-capita* availability of fruit resources in each stratum.

DEMOGRAPHY

We used DNA-based mark–recapture to estimate demographic parameters, and thereby population growth rate, which provides a measure of the mean individual fitness (Fisher 1930) for each stratum. Grizzly bear hair samples were collected over a period of 8 years (2006–2013) using two types of genetic sampling: lured bait sites and rub objects. A total of 482 bait site and 406 rub object locations were sampled between 2006 and 2013, for a total of 1066 bait site sessions and 2748 rub object sessions. In total, we recorded 1346 mark and recapture events (unique bear-session detection events) of 489 individuals. Further details on field sampling and individual identification through multilocus microsatellite genotyping can be found in Appendix S3.

Capture histories were constructed for each stratum from DNA capture–recapture data and analysed using a Pradel robust design model (PRDM, Pradel 1996; Nichols *et al.* 2000) for open populations implemented in program MARK (White & Burnham 1999) using the RMark package (Laake 2013) accessed in program R. We estimated apparent survival (ϕ), apparent recruitment (f), realized population growth (λ), abundance (N) and probability of capture (p) for each of the three strata (North, Trap, and South). The PRDM is a combination of the Pradel estimator (Pradel 1996), which estimates demographic parameters of open populations (Nichols & Hines 2002), and the Huggins formulation of the closed population design, used to estimate detection probabilities and population size (Huggins 1991). The robust design is based on multiple sampling sessions (years, in our case), and within each sampling session, multiple secondary sessions are nested (Gardner *et al.* 2010). The annual capture histories for each stratum are comprised of two bait site and one rub tree session per year, except in 2012, when we only deployed rub trees and had four secondary sessions. We split rub trees and bait sites into separate sessions as these traps are known to have different capture probabilities (Boulanger *et al.* 2008b; Lamb, Walsh & Mowat 2016).

The PRDM estimates 'apparent' survival because actual mortality cannot be distinguished from emigration (i.e. in both cases, the bear is never recaptured in the population). Similarly, 'apparent' recruitment is estimated because detection of a new individual is indistinguishable from the detection of an individual moving into the stratum (i.e. in both cases, a new bear is captured that had not been previously detected). The resulting

measure of realized population growth (λ) is simply the sum of the probability of entering the population [apparent recruitment (f)] and the probability of remaining in the population [apparent survival (ϕ)] (Nichols & Hines 2002). We met all assumptions of the PRDM (for information on assumptions and further detail on modelling methods, see Appendix S3). Statistical comparisons between parameters were made using two-tailed Z tests. We conducted a sensitivity analysis to ensure our demographic inferences were not affected by buffer choice (Appendix S5).

The province of British Columbia has kept records of all known human-caused grizzly bear mortalities since 1978 as part of compulsory inspection. The data base includes the date, location and cause of death, as well as the sex, age and skull size for each individual. We used these data in conjunction with the abundance estimates generated by our capture–recapture model to calculate annual human-caused mortality rates for all strata. For each stratum, we calculated mortality rates using the average abundance of grizzly bears across all years and averaged annual hunter and non-hunter mortalities using mortality data between 2006 and 2014.

Although reporting of grizzly bear mortalities is mandatory, approximately half of all non-hunting, human-caused grizzly bear mortalities are not reported (McLellan, Hovey & Mace 1999). To account for this, we inflated all reported non-hunting mortalities by a factor of two following the estimate from McLellan, Hovey & Mace (1999), which we later validated using the estimated survival rates for each stratum (Appendix S4) as these estimates are generated independent of the mortality data. Statistical comparisons of mortality rate between strata were made using analysis of variance (ANOVA) and the associated *post hoc* Tukey HSD test (further information on methods, equations and validation can be found in Appendix S3).

MOVEMENT

One of the limitations of apparent recruitment estimates is ambiguity between recruitment of cubs and movements from elsewhere. We combined information from our mark–recapture sampling with records of human-killed bears from the compulsory inspection data base to identify the effects of movement between strata on apparent survival and recruitment for each stratum. We successfully genotyped samples from 102 of the 163 recorded human-caused grizzly bear mortalities in the study area since 2006, and we matched these to genotypes of bears in our capture–recapture sample using a genetic match test of all nine microsatellite markers. Our capture–recapture sample included 56 of the 102 bears that were killed and produced a genotype. Using these data, we investigated the movement of bears that were killed and used a two-tailed proportion test in R to test whether there were more bears entering the Trap than leaving it (further information on methods and equations used can be found in Appendix S3). We chose to use the movements of bears that were first detected live and later identified as a mortality in the compulsory inspection data base (live–dead), as opposed to bears that were still alive in our population (live–live, i.e. caught live and still alive at last capture). Using the movements of the live–dead bears required us to assume less about the endpoint of the bear's movement since the location of the mortality is final, and there could be no further dispersal.

Dispersal in grizzly bears is male and subadult biased (McLellan & Hovey 2001b; Proctor & McLellan 2004; Graham &

Stenhouse 2014). Therefore, if bears move from elsewhere into the Trap, we predicted the age structure in the trap to be skewed towards young male bears. We used the human-killed bear data to measure the age structure, and our population estimates to measure sex ratios of bears in each stratum. Statistical comparisons between strata were made using analysis of variance (ANOVA) and the associated *post hoc* Tukey HSD test (further information on methods, equations and validation can be found in Appendix S3).

Results

HABITAT ATTRACTIVENESS

The best huckleberry model included per cent of area burned, per cent sand, average winter temperature, precipitation as snow, canopy cover, average pH, slope and solar heat load (Table S3). The best buffaloberry model was similar to that found for huckleberry, but the summer climate better explained occurrence for this species (Table S3). Both models displayed good model accuracy for predicting occurrence using testing data (AUC, huckleberry = 0.855 ± 0.016 , buffaloberry = 0.791 ± 0.031). These are the most predictive models published for either species in the Kootenay Region (Hobby & Keefer 2010).

Huckleberry occurrence decreased with latitude, while buffaloberry was more evenly distributed (Fig. S1). Huckleberry and buffaloberry showed very little spatial overlap with <6% of berry occurrence cells containing both species.

Fruit-producing shrubs (huckleberry and buffaloberry) covered a greater proportion of the Trap stratum (0.44) than the North (0.29) or South (0.37) strata. Similarly, the *per-capita* availability of these species was highest in the Trap stratum (24.8 km² per bear) than the North (7.0 km² per bear) or South (9.3 km² per bear) strata (Fig. 3a).

DEMOGRAPHY

Estimates of grizzly bear demography across strata were within the standard target for robust estimates of population size (Pederson *et al.* 2012), a coefficient of variation (CV) <20% (CV = 7.2–16.6%, Table 1). Average annual capture probabilities were similar between strata and to previous work on this species (Trap = 0.35 ± 0.04 , North = 0.40 ± 0.04 and South = 0.40 ± 0.05 ; Boulanger *et al.* 2008a). Covariates that best explained variations in capture probability included sex of the bear, the type of trap used (rub object or bait site), trapping effort, time of year, year of sampling and a project-specific covariate (full model selection table can be found in Appendix S4, Table S6). Males had higher capture probabilities than females, and bait sites detected more bears than rub objects with effort (trap nights) being positively related to detection (Lamb *et al.* 2016).

Grizzly bears attained the highest estimated densities in areas of low mortality (Fig. 3d, Table 1). Estimated human-caused mortality rates were approximately three

times greater in the Trap than in adjacent strata ($P \leq 0.0001$ between all strata except North–South where $P = 0.91$, Fig. 3d). Estimated apparent survival rates were lower in the Trap ($\phi = 0.65 \pm 0.053$) than in surrounding areas (North $\phi = 0.79 \pm 0.020$, and South $\phi = 0.78 \pm 0.037$), and also differed statistically in Trap–North and Trap–South comparisons ($P \leq 0.05$) but not in North–South comparisons ($P = 0.79$) (Fig. 3b). Validation of non-reporting rate suggested the non-hunter *2 correction was conservative for the Trap (Mowat & Lamb 2016, Appendix S4).

Apparent recruitment rates were highest in the Trap ($f = 0.27 \pm 0.058$), which was marginally higher than in the North ($f = 0.16 \pm 0.023$, $P = 0.09$), but not higher than in the South ($f = 0.19 \pm 0.038$, $P = 0.25$, Fig. 3c), with no statistical significant difference detected between the North and South ($P > 0.56$). All strata demonstrated annual growth rates below 1: Trap = 0.92 ± 0.040 , North = 0.95 ± 0.023 and South = 0.97 ± 0.037 , $P > 0.05$ for all comparisons.

MOVEMENT

A large proportion of the mortalities that occurred in the Trap stratum were bears previously detected in the North (26%) or South (18%), while few North (5%) and South (0%) strata mortalities were bears first detected in the Trap stratum. Of the movements we documented, the proportion of bears that moved into the Trap and died (0.43) was greater than those leaving the Trap and dying (0.04) ($P = 0.003$, Fig. 3f,g). This difference is not simply a function of decreased survival rates in the Trap because there were 10 times more detections of bears that moved into and died in the Trap than moved out of the trap and died, but only 1.6 times greater mortality risk in the Trap compared to adjacent strata (Fig. 3b). The remaining proportion of movements (0.53) were within individual strata.

Average age of bears killed was approximately 3 years younger in the Trap (mean = 6.4 ± 0.7 years old) than in the backcountry regions (North; mean = 9.8 ± 1.0 and South; mean = 10.1 ± 1.3 years old, Fig. 3e). Bears killed in the Trap were younger ($P < 0.01$) than in surrounding strata, even after accounting for the different sources of mortalities between strata (Fig. 3d, Appendix S4). No age differences were detected between the North and South strata ($P = 0.99$) or between sexes ($P = 0.56$).

Average annual sex ratio in the Trap was 1.17 (± 0.20) males to every female bear, but only 0.69 (± 0.04) and 0.85 (± 0.07) males per female in the North and South, respectively. Sex ratios were different between the North and Trap ($P = 0.02$), but not between the South and Trap ($P = 0.13$) or the North and South ($P = 0.07$). Over 60% of bears killed in the Trap were subadults or cubs (<6 years of age), while bears of these age classes only composed 38 and 24% of the recorded mortalities in North and South, respectively. The

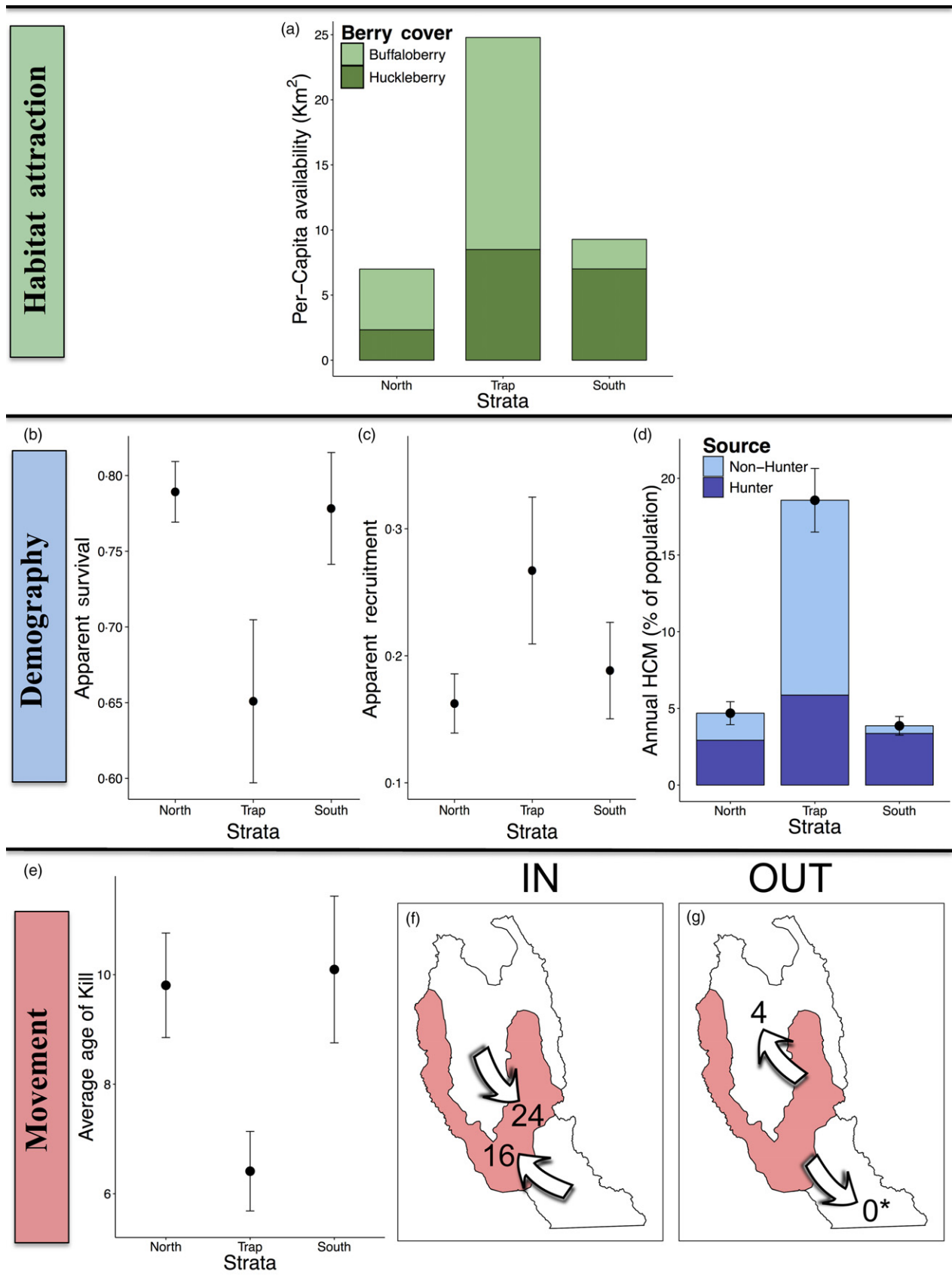


Table 1. Estimated population sizes for each stratum from the Huggins estimator, including measures of confidence (SE = standard error, CV = coefficient of variation), the area of each strata and the resulting grizzly bear density per 1000 km². *Density of grizzly bears predicted to use the stratum from the Huggins closed estimator divided by the stratum area; this does not account for lack of population closure and is thus biased high (c. 17% as calculated by Mowat & Lamb 2016). We retain the measure for comparison between strata only

Stratum	Population size	SE	CV (%)	Area (km ²)	Density* (bears/1000 km ²)
North	166	11.9	7.2	3983	41.7
Trap	66	11	16.6	3584	18.5
South	88	10.5	11.9	2190	40.3

proportion of subadult and cubs killed was greater in the Trap than in the other areas ($P < 0.001$).

Discussion

We show that grizzly bears face an ET produced by human-caused mortality in an area of high human density and rich food resources for bears. This trap produces realized population declines of approximately 8% per year in the Trap and at least 1.5% per year in source populations (North and South). Specifically, we demonstrate that the ET had (i) greater cover and *per-capita* availability of fruit-producing shrubs [that are selected by grizzly bears and increase fitness in the absence of humans (McLellan 2015)]; (ii) greatly reduced survival and insufficient compensation in recruitment to prevent population declines; and (iii) compensatory immigration of individuals into the ET from adjacent strata at a ratio of 10 entering the ET and dying to every 1 leaving and dying. Overall, highly attractive habitat in close proximity to lethal human settlement created a 'severe' trap (Robertson, Rehage & Sih 2013; Hale, Treml & Swearer 2015) that exacerbated demographic loss in source populations.

Two small areas within the Trap area were sampled during 2002 and 2003, and average density for these areas was 36.5/1000 km² (Mowat *et al.* 2013), much higher than we found a decade later (18.5/1000 km²). Projecting the 2002/2003 density through time using the growth rate estimated here for the Trap ($\lambda = 0.92$) to the median year of this study suggests a density similar to our estimated density (density projected = 18.7/1000 km²). We speculate the cause of the decline in the Trap is an interactive effect of high human-

caused mortality and multiple successive years of fruit crop failure (2004–2007) and poor fruit production (2008, 2010 and 2012, McLellan 2015) producing increased human–bear conflicts (Pease & Mattson 1999; Gunther *et al.* 2004) and reduced reproduction (McLellan 2015).

Between 2006 and 2014, human-caused non-hunting mortalities in the Trap were largely due to collisions with vehicles and trains (54%), with control kills due to human–bear conflicts and illegal kills accounting for 33% and 13%, respectively. The majority of human-caused mortalities in the Trap are attributed to non-hunting sources (68%), an exceptionally pervasive mortality source that cannot be mitigated through simple regulatory changes, as is done with hunting. Since the 1980s, non-hunting bear mortalities have steadily increased in the Trap and surrounding areas (Mowat *et al.* 2013) and across the species range (Can *et al.* 2014), likely due to increasing human settlement and development in grizzly bear habitat.

High mortality rates can create vacancies that are subsequently occupied by young dispersers. Our results are consistent with the compensatory immigration hypothesis (Cooley *et al.* 2009); bears killed in the Trap were on average 3 years younger than those killed outside the Trap, and the proportion of males was higher in the Trap than elsewhere. This young and male-skewed composition of individuals in the Trap suggests dispersing juvenile males filled vacancies in this area, and areas with few females and many young males have much lower reproductive potential than areas with more females of reproductive age. Our minimum estimate of four bears moving into the Trap stratum per year represents 66% of the difference between apparent recruitment in the Trap and the mean recruitment of the North and South strata. Thus, recruitment in the Trap is, at most, only marginally greater than in the other two strata, with the majority of this difference in apparent recruitment (at minimum, two-thirds) due to individuals moving in and occupying vacancies.

Compensatory reproduction may account for a small portion (maximum 33%) of the increased apparent recruitment observed in the Trap, relative to other strata, but is clearly not sufficient to meet replacement nor deter the immigration of individuals from elsewhere. We acknowledge that social structure can alter the spatiotemporal distribution of subordinate individuals, where subadults and females with cubs may avoid potentially infanticidal males (Nevin & Gilbert 2005; Elfstrom *et al.*

Fig. 3. Information required to classify the Trap stratum as an ecological trap. Habitat attraction: (a) *per-capita* availability of huckleberry and buffalobery shrubs within each stratum. High coverage and availability of these key nutritional resources represents attractive habitats for grizzly bears. Demography: (b) apparent survival (survival + emigration), (c) apparent recruitment (recruitment + immigration) and (d) annual human-caused mortality (HCM) of each stratum by mortality source. Movement: (e) average age of bears killed by humans in each strata, (f and g) decadal flow of bears between strata that are subsequently killed projected using a combination of genetic capture data and mortality information, (f) IN represents flow of individuals into the Trap stratum that were killed, and (g) OUT represents flow out of the Trap stratum that were killed. Overall, the flow ratio of IN:OUT is 10:1.

2014). However, we believe any degree of socially driven spatial structure will occur within a home range, and we have not found support for sexually selected infanticide (SSI) in our study area (McLellan 2005). The ET outlined here represents a population-level phenomenon that cannot be explained by social factors alone and must be driven by population dynamics, food availability, habitat selection and perceived fitness outcomes. Individuals likely spend more time in the Trap because the *per-capita* fruit resources are more abundant, and due to increased proximity to humans, mortality is higher. Additional food resources present in the Trap, but not the North or South, include spawning kokanee salmon (*Oncorhynchus nerka*) and anthropogenic food sources (fruit trees, livestock and garbage), which likely act to bring bears and humans into direct contact as many of these resources are in close proximity to human settlements. Similar landscape-level redistributions of individuals due to food resources near human settlements have been observed in black bears (*Ursus americanus*, Beckman & Berger 2003).

Although the dispersal capability of wide-ranging species is large, it can be impeded by habitat fragmentation (Holderegger & Di Giulio 2010). Proctor *et al.* (2012) identified genetic differentiation and low dispersal across highways and settled areas throughout the southern grizzly distribution – including our study area – and highlighted a correlation between genetic distance and the degree of human settlement and highway traffic. Here, we document the causal mechanisms fracturing demographic connectivity in the Trap, a key connectivity corridor for the largest southern peninsular grizzly bear population in North America (Fig. 1). Specifically, our findings suggest gametes are not shared between the North and South because: (i) attractive food provides little motivation for dispersers to move through the Trap, and the longer individuals stay in the Trap the more likely they are to be killed by humans; (ii) movements into the Trap are largely by younger bears that are likely not motivated to move into the North or South and compete for mates, food and space with the older bears occupying these areas; and (iii) high female mortality rates in the Trap mean that many females are too young to have a litter, which results in low recruitment in the Trap and contributes to low dispersal out of the Trap. The behavioural and demographic mechanisms identified here explain the genetic differentiation observed by Proctor *et al.* (2012) despite documentation of occasional movements across proposed fracture areas. These mechanisms may also explain population fractures in other wide-ranging species that are similarly susceptible to human-caused mortality and genetic isolation.

In classic source–sink dynamics, source habitats produce dispersers because local recruitment exceeds replacement (Pulliam 1988). The areas we considered as sources supplied dispersers to the Trap, but these sources were declining, although more slowly than the Trap. Cooley *et al.* (2009) observed a similar pattern, where juvenile cougars (*Puma concolor*) dispersed from source habitat

where the population was declining ($\lambda < 1$) to an area with high vacancy rates caused by human predation. The authors proposed that this dispersal was due to the intrinsic nature of dispersal in cougar populations. Bears likely disperse due to an intrinsic dispersal mechanism as well (McLellan & Hovey 2001b), but may disperse much less if intraspecific competition is low, as is likely in the Trap. Although lower densities may indicate lower intraspecific competition, male-skewed sex ratios may increase SSI in the Trap; however, investigations into the effects of SSI in our region of study and elsewhere in North America do not support SSI as a strong limiting factor across a range of male sex ratios (Miller, Sellers & Keay 2003; McLellan 2011).

We note that emigration out of a declining population due to an ET has the potential to create a severe conservation concern if source populations are small and the ET is exceptionally attractive. In the case of the South strata, these bears face multiple threats and sanctuaries as they range beyond BC into Alberta, and Montana in the United States. Bears in the south-east corner of BC provide a population source for potential ETs on agricultural land to the west in Alberta (Northrup, Stenhouse & Boyce 2012; Morehouse & Boyce 2016); however, demographic rescue may be compromised if these core populations are demographically overdrawn. The spatial scale at which an ET affects adjacent, secure populations should be related to the dispersal capability of the species affected. Wide-ranging apex consumers are especially vulnerable to anthropogenic ETs due to a lack of natural predators reducing evolutionary vigilance in the face of a human threat. As such, the large dispersal capabilities of these species should produce large-scale demographic consequences in the presence of an ET, as noted by Hale, Trembl & Swearer (2015). We documented a number of long-distance movements into the Trap, including a 58-km displacement of one individual initially detected in the North that was subsequently killed in the Trap. These dynamics highlight the insidious and far-reaching demographic effects of ETs for apex consumers, where declines are further exacerbated due to the presence of ETs.

The idea that the evolutionary cues animals use to select habitats can be poorly matched with novel conditions is the basis for ETs (Robertson, Rehage & Sih 2013). ETs are most lethal when they arise rapidly (in evolutionary time) and, as a result, many ETs are associated with anthropogenic disturbance [human-induced rapid ecological change (HIREC); Robertson, Rehage & Sih 2013]. Our findings demonstrate the deleterious effects of human settlement on grizzly bear demography, which are exacerbated by attractive habitat creating an ET. Due to the large home ranges of grizzly bears and movement of young bears, the effects of localized mortality in our study area resulted in demographic consequences for areas far removed from the Trap. Furthermore, the ability of individuals to identify and respond to the consequences of occupying the Trap is low, due to the Trap causing death (a non-repeating event).

This is in contrast to a failed reproduction event [another potential consequence of occupying an ET, Dwernychuk & Boag (1972)], which could afford an individual a chance to alter their behaviour to habitat cues during a subsequent reproduction attempt (Battin 2004; Hale, Treml & Swearer 2015). To date, the drastic range contractions for grizzly bears have been tightly linked to human impact and associated mortality (Fig. 1). Focusing on mortality sources that can be immediately reduced (e.g. hunting) may help alleviate the broad population consequences of the Trap in the short term, but addressing the larger and more insidious sources of non-hunting mortality (e.g. road, rail and human–bear conflicts) will be required for long-term viability (Mowat & Lamb 2016). However, mitigation of these non-hunting mortality sources, such as fencing towns or rail and road ways, can come at high monetary and ecological costs unless connectivity is maintained through alternate means (Holderegger & Di Giulio 2010; Sawaya 2014). More broadly, the population dynamics presented here highlight the imperative need to maintain the integrity of intact landscapes that provide critical habitat for grizzly bears and refuge from human development and associated human–bear conflicts.

An ET where food is the attractant is a specialized case of the more general evolutionary trap, where any resource (mate, food or habitat) is perceived as attractive despite reduced fitness (Robertson, Rehage & Sih 2013). The coexistence of humans and apex consumers is difficult and often incompatible (Can *et al.* 2014), and the occurrence of such species within human-dominated areas highlights the evolutionary mismatch between perceived resource quality and realized fitness. In particular, range reductions have been documented in all species in the order *Carnivora* due to human impacts (Ripple *et al.* 2014), and the expansion of human settlement continually brings the human–carnivore conflict into new arenas. There is an urgent need to mitigate human–carnivore conflict as all successful cases of recovery include mitigation of human activity, not the evolutionary adaptation of carnivores to human threats.

Authors' contributions

CTL conducted a portion of the field work and all analyses and led the writing of the manuscript with suggestions and idea developments from GM, BNM, SEN, and SB. GM is the Principal Investigator on the South Rockies Grizzly Bear Project, collected the majority of data and provided direction and comments; BNM provided insight into the population dynamics discussed here and provided telemetry data used to validate attraction indices and strata boundaries; SEN aided in the creation of the berry occurrence models and provided insights and comments throughout; SB provided insights and comments as this work developed.

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Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.bg2s4> (Lamb *et al.* 2016).

References

- Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716–723.
- Apps, C.D., Mclellan, B.N., Woods, J.G. & Proctor, M.F. (2004) Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management*, **68**, 138–152.
- Apps, C.D., Mclellan, B., Bateman, B. & Serrouya, R. (2007) *Evaluating and Refining Grizzly Bear Forested Buffer Habitat Management Guidelines*. Prepared for the Province of British Columbia.
- Balme, G.A., Slotow, R. & Hunter, L.T.B. (2010) Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, **13**, 315–323.
- Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, **18**, 1482–1491.
- Beckman, J.P. & Berger, J. (2003) Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy*, **84**, 594–606.
- Boulanger, J. & Stenhouse, G.B. (2014) The impact of roads on the demography of grizzly bears in Alberta. *PLoS ONE*, **9**, e115535.
- Boulanger, J., Kendall, K.C., Stetz, J.B., Roon, D.A., Waits, L.P. & Paetkau, D. (2008a) Multiple data sources improve DNA-based mark–recapture population estimates of grizzly bears. *Ecological Applications*, **18**, 577–589.
- Boulanger, J., MacHutchon, G., Stenhouse, G.B., Proctor, M., Cranston, J. & Paetkau, D. (2008b) *Grizzly Bear Population and Density Estimates for Alberta Bear Management Unit 6 and British Columbia Management Units 4-1, 4-2, and 4-23 (2007)*. Report Prepared for the Alberta Sustainable Resource Development, Fish and Wildlife Division, British Columbia Ministry of Forests and Range, British Columbia Ministry of Environment, and Parks Canada.
- Can, O.E., D'Cruze, N., Garshelis, D.L., Beecham, J. & Macdonald, D.W. (2014) Resolving human–bear conflict: a global survey of countries, experts, and key factors. *Conservation Letters*, **7**, 501–513.
- Cooley, H.S., Wielgus, R.B., Koehler, G. & Maletzke, B. (2009) Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. *Animal Conservation*, **12**, 321–328.
- COSEWIC (2012) *COSEWIC Assessment and Status Report Grizzly Bear Ursus Arctos in Canada*. COSEWIC, Ottawa, ON, Canada.
- Darwin, C. (1859) *The Origin of the Species by Means of Natural Selection*. John Murray, London, UK.
- Dwernychuk, L.W. & Boag, D.A. (1972) Ducks nesting in association with gulls – an ecological trap? *Canadian Journal of Zoology*, **50**, 559–563.
- Elftstrom, M., Zedrosser, A., Jerina, K., Stoen, O.G., Kindberg, J., Budic, L. *et al.* (2014) Does despotic behavior or food search explain the occurrence of problem brown bears in Europe? *Journal of Wildlife Management*, **78**, 881–893.
- Fawcett, T. (2006) An introduction to ROC analysis. *Pattern Recognition Letters*, **27**, 861–874.
- Fisher, R. (1930) *The Genetical Theory of Natural Selection*. Oxford University Press, New York, NY, USA.
- Fretwell, S.D. & Lucas, H.L.J. (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **14**, 16–36.
- Gardner, B., Reppucci, J., Lucherini, M. & Royle, J.A. (2010) Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology*, **91**, 3376–3383.

- Graham, K. & Stenhouse, G. (2014) Home range, movements, and denning chronology of the grizzly bear (*Ursus arctos*) in West-Central Alberta. *The Canadian Field-Naturalist*, **128**, 223–234.
- Gunther, K.A., Haroldson, M.A., Frey, K., Cain, S.L., Copeland, J. & Schwartz, C.C. (2004) Grizzly bear–human conflicts in the Greater Yellowstone ecosystem, 1992–2000. *Ursus*, **15**, 10–22.
- Hale, R. & Swearer, S.E. (2015) Ecological traps: current evidence and future directions. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **283**, 20152647.
- Hale, R., Treml, E.A. & Swearer, S.E. (2015) Evaluating the metapopulation consequences of ecological traps. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **282**, 20142930.
- Hobby, T. & Keefer, M. (2010) A black huckleberry case study in the Kootenays region of British Columbia. *Journal of Ecosystems and Management*, **11**, 52–61.
- Holderegger, R. & Di Giulio, M. (2010) The genetic effects of roads: a review of empirical evidence. *Basic and Applied Ecology*, **11**, 522–531.
- Huggins, R.M. (1991) Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics*, **47**, 725–732.
- Laake, J.L. (2013) *RMark: An R Interface for Analysis of Capture-Recapture Data with MARK*. AFSC Processed Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA, USA.
- Lamb, C.T., Walsh, D. & Mowat, G. (2016) Factors influencing detection of grizzly bears at genetic sampling sites. *Ursus*, **27**, 31–44.
- Lamb, C.T., Mowat, G., McLellan, B.N., Nielsen, S.E. & Boutin, S. (2016) Data from: Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.bg2s4>.
- Lopez-Alfaro, C., Robbins, C.T., Zedrosser, A. & Nielsen, S.E. (2013) Energetics of hibernation and reproductive trade-offs in brown bears. *Ecological Modelling*, **270**, 1–10.
- Mattson, D. & Merrill, T. (2002) Extirpations of Grizzly Bears in the Contiguous United States, 1850–2000. *Conservation Biology*, **16**, 1123–1136.
- McLellan, B. (1989) Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. *Canadian Journal of Zoology*, **67**, 1856–1860.
- McLellan, B. (2005) Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus*, **16**, 141–156.
- McLellan, B. (2011) Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*). *Canadian Journal of Zoology*, **558**, 546–558.
- McLellan, B.N. (2015) Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *Journal of Wildlife Management*, **79**, 749–765.
- McLellan, B. & Hovey, F. (2001a) Habitats selected by grizzly bears in a multiple use landscape. *The Journal of wildlife management*, **65**, 92–99.
- McLellan, B.N. & Hovey, F.W. (2001b) Natal dispersal of grizzly bears. *Canadian Journal of Zoology*, **79**, 838–844.
- McLellan, B., Hovey, F. & Mace, R. (1999) Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *The Journal of wildlife management*, **63**, 911–920.
- van der Meer, E., Fritz, H., Blinston, P. & Rasmussen, G.S.A. (2013) Ecological trap in the buffer zone of a protected area: effects of indirect anthropogenic mortality on the African wild dog *Lycaon pictus*. *Oryx*, **48**, 285–293.
- MFLNRO (2012) *British Columbia Grizzly Bear Population Estimate for 2012*. MFLNRO, Victoria, Canada.
- Miller, S., Sellers, R. & Keay, J. (2003) Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus*, **14**, 130–152.
- Morehouse, A.T. & Boyce, M.S. (2016) Grizzly bears without borders: spatially explicit capture recapture in southwestern Alberta. *Journal of Wildlife Management*, **80**, 1152–1166.
- Morrison, J.C., Sechrest, W., Dinerstein, E., Wilcove, D.S. & Lamoreux, J.F. (2007) Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy*, **88**, 1363–1380.
- Mowat, G. & Lamb, C.T. (2016) *Population Status of the South Rockies and Flathead Grizzly Bear Populations in British Columbia, 2006–2014*. Province of British Columbia, Nelson, BC, Canada.
- Mowat, G., Efford, M., McLellan, B.N. & Nielsen, S. (2013) *South Rockies & Flathead Grizzly Bear Monitoring Final Report 2006–2011*. Prepared for Province of British Columbia. Nelson, BC, Canada.
- Nevin, O.T. & Gilbert, B.K. (2005) Perceived risk, displacement and refuging in brown bears: positive impacts of ecotourism? *Biological Conservation*, **121**, 611–622.
- Nichols, J. & Hines, J. (2002) Approaches for the direct estimation of u, and demographic contributions to u, using capture–recapture data. *Journal of Applied Statistics*, **29**, 539–568.
- Nichols, J.D., Hines, J.E., Lebreton, J. & Pradel, R. (2000) Estimation of contributions to population growth: a reverse-time capture–recapture approach. *Ecology*, **81**, 3362–3376.
- Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006) A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, **130**, 217–229.
- Nielsen, S., Boyce, M., Stenhouse, G. & Munro, R. (2002) Modeling grizzly bear habitats in the yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus*, **13**, 45–56.
- Nielsen, S., Boyce, M., Stenhouse, G. & Munro, R. (2003) Development and testing of phenologically driven grizzly bear habitat models. *Ecoscience*, **10**, 1–10.
- Nielsen, S., Johnson, C., Heard, D. & Boyce, M. (2005) Can models of presence–absence be used to scale abundance? Two case studies considering extremes in life history. *Ecography*, **2**, 197–208.
- Nielsen, S., McDermid, G., Stenhouse, G.B. & Boyce, M.S. (2010) Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy–abundance and habitat selection in grizzly bears. *Biological Conservation*, **143**, 1623–1634.
- Northrup, J.M., Stenhouse, G.B. & Boyce, M.S. (2012) Agricultural lands as ecological traps for grizzly bears. *Animal Conservation*, **15**, 369–377.
- Pease, C. & Mattson, D. (1999) Demography of the Yellowstone grizzly bears. *Ecology*, **80**, 957–975.
- Pederson, J.C., Bunnell, K.D., Conner, M.M. & McLaughlin, C.R. (2012) A robust-design analysis to estimate American black bear population parameters in Utah. *Ursus*, **23**, 104–116.
- Pradel, R. (1996) Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics*, **52**, 703–709.
- Proctor, M. & McLellan, B. (2004) Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Canadian Journal of Zoology*, **118**, 1108–1118.
- Proctor, M.F., Paetkau, D., McLellan, B.N., Stenhouse, G.B., Kendall, K.C., Mace, R.D., et al. (2012) Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs*, **180**, 1–46.
- Pulliam, H. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652–661.
- R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Core Team, Vienna, Austria.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al. (2014) Status and ecological effects of the world's largest carnivores. *Science (New York, N.Y.)*, **343**, 1241484.
- Robertson, B.A. & Hutto, R.L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, **87**, 1075–1085.
- Robertson, B.A., Rehg, J.S. & Sih, A. (2013) Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology and Evolution*, **28**, 552–560.
- Rovang, S.B. (2013) *University of Alberta Factors Affecting the Detectability and Eastern Distribution of Grizzly Bears in Alberta, Canada by Master of Science in Department of Renewable Resources*. University of Alberta, Edmonton, AB, Canada.
- Runge, J.P., Runge, M.C. & Nichols, J.D. (2006) The role of local populations within a landscape context: defining and classifying sources and sinks. *The American Naturalist*, **167**, 925–938.
- Sawaya, M. (2014) Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **281**, 20131705.
- Welch, C., Keay, J., Kendall, K. & Robbins, C. (1997) Constraints on frugivory by bears. *Ecology*, **78**, 1105–1119.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, S120–S139.
- Wildlife Conservation Society – WCS, and Center for International Earth Science Information Network – CIESIN – Columbia University, (2005) *Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Influence Index (HII) Dataset (Geographic)*. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY, USA.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary berry occurrence methods and results.

Appendix S2. Supplementary berry occurrence methods and results.

Appendix S3. Supplementary demography methods.

Appendix S4. Supplementary demography methods.

Appendix S5. Sensitivity.

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Evaluating the metapopulation consequences of ecological traps

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Ecological traps occur when environmental changes cause maladaptive habitat selection. Despite their relevance to metapopulations, ecological traps have been studied predominantly at local scales. How these local impacts scale up to affect the dynamics of spatially structured metapopulations in heterogeneous landscapes remains unexplored. We propose that assessing the metapopulation consequences of traps depends on a variety of factors that can be grouped into four categories: the probability of encounter, the likelihood of selection, the fitness costs of selection and species-specific vulnerability to these costs. We evaluate six hypotheses using a network-based metapopulation model to explore the relative importance of factors across these categories within a spatial context. Our model suggests (i) traps are most severe when they represent a large proportion of habitats, severely reduce fitness and are highly attractive, and (ii) species with high intrinsic fitness will be most susceptible. We provide the first evidence that (iii) traps may be beneficial for metapopulations in rare instances, and (iv) preferences for natal-like habitats can magnify the effects of traps. Our study provides important insight into the effects of traps at landscape scales, and highlights the need to explicitly consider spatial context to better understand and manage traps within metapopulations.

1. Introduction

Humans are altering ecosystems at significantly faster rates than natural forms of environmental change. This is referred to as human-induced rapid environmental change (HIREC) [1], and it leads to profound changes to habitat quality and quantity. Whether dispersing animals can continue to adaptively select suitable habitats in the face of HIREC is an important question, particularly if the cues used by animals during habitat selection become uninformative of habitat quality. This breakdown between habitat preferences and quality can cause ecological traps, when animals select habitats that provide fitness outcomes inferior to other nearby habitats [2–4].

Ecological traps were originally described following studies with birds [5], but occur across a wide range of taxa (for examples, see [3]). Perhaps the most compelling case is the attraction of insects to artificial sources of polarized light (e.g. roads) and their subsequent death upon landing [6]. Traps can also have sub-lethal effects; for example, red-backed shrikes in northwest Europe prefer open areas created by farming, where their reproductive performance is lower than in nearby forests [7]. Given the mounting evidence across taxa and ecosystems, ecological traps are likely to increase the risk of extinction and loss of biodiversity, with important implications for conservation and management [8]. This has motivated efforts to better understand how traps form and to describe their potential effects (e.g. [2–4,9–12]). Much of this effort, however, has been at the scale of local populations, such as testing which of a few habitat patches may be traps (e.g. studies within [4]), or modelling the effects of traps in landscapes with only two habitat types (i.e. ‘low’ and ‘high’ quality). Furthermore, while the impacts of traps will depend on their severity (i.e. attractiveness, fitness costs) [11,13], the local dynamics of traps play out within the context of landscapes that may have a mosaic of different-quality habitats, especially as they are modified under HIREC. There are also reasons why inferring the wider-scale consequences of traps from

local studies may be problematic, such as if habitat preferences are evaluated at a small number of locations that are poorly representative of those available [14]. This suggests that further insight could be gained by evaluating ecological traps within a broader, regional context.

The metapopulation concept is a standard ecological paradigm for exploring the dynamics and evolution of organisms in spatially structured landscapes [15]. In most ecosystems, local patches vary in habitat quality, which often influences vital demographic rates and thus the persistence of local populations [16,17]. This can lead to source–sink dynamics, where poor-quality habitats cannot support local populations without replenishment from other patches [18,19]. The concepts of ecological traps and source–sink dynamics are related; a sink is analogous to an ecological trap if it is preferred over other patches, but source–sink theory does not incorporate the potential for maladaptive habitat selection [13], a key characteristic of a trap. Whether ecological traps occur, and whether their presence reduces the growth rate and/or persistence of metapopulations, will ultimately be determined by how dispersal and habitat selection, and their associated fitness consequences, are altered across landscapes. At present, our ability to assess how traps may compromise metapopulations and how their effects can be best managed is hindered by a limited understanding of how traps impact spatially structured populations across a landscape.

(a) A framework for assessing the landscape scale consequences of ecological traps

We develop a conceptual framework integrating metapopulation theory, movement ecology and sensory biology to assess the consequences of ecological traps for metapopulations within spatially explicit landscapes. We propose that the factors likely to determine the consequences of traps for metapopulations can be grouped into four main categories as follows.

(i) The probability of encounter

This will depend on both the physical environment and the life-history traits of organisms. Animals will encounter traps more frequently when they represent a larger proportion of available habitat. The underlying topology of the landscape is likely to affect metapopulation persistence when traps are present, as has been demonstrated in studies without traps [20,21]. The characteristics of trap patches relative to other habitat patches will also probably be important. For example, large traps may represent larger ‘targets’ for dispersers, or traps that are isolated from other patches in the network may be encountered less frequently [22–24].

Their dispersal and perceptual ability will affect the probability that animals encounter traps (electronic supplementary material, appendix S1). Range-restricted species may be highly susceptible [8], whereas vagile species may encounter traps more frequently but have greater capability of ‘escaping’ by moving to more favourable habitats. Migratory species with obligate habitat transitions may be particularly susceptible. Finally, animals with a larger perceptual range [25] may be attracted to habitats from greater distances, potentially increasing the frequency with which they encounter traps.

(ii) Likelihood of selection

Animals may exhibit a preference for traps (a ‘severe’ trap), or equally prefer traps and non-traps (an ‘equal-preference’ trap) [3]. In both cases, animals will select traps more frequently if their dispersal is uninformed (i.e. an imperfect knowledge of the environment) and they rely on indirect habitat selection cues acting as proxies for habitat quality [8] (electronic supplementary material, appendix S1). Animals that use multiple cues (either simultaneously or sequentially) to locate and assess habitats (e.g. [26]) may be less susceptible, as they will require multiple stimuli to incorrectly indicate high habitat quality. Physiological changes to dispersers may also increase the probability that animals will select traps; animals in poor physiological condition or under tight time constraints will generally become less choosy in terms of selecting mates or habitats (see [27] and references within), or more likely to choose poor-quality habitat [28].

Natal experience influences habitat preferences for a wide range of taxa including insects, fish, mammals and birds [27,29,30], and almost always leads to a preference for natal-like habitats, known as natal habitat preference induction (NHPI) [30]. Although NHPI could weaken the effects of traps [11], we suggest that it could equally cause them, if animals raised in poor-quality natal habitats select similar ones later in life. For example, common loons in Wisconsin select lakes similar to their natal site in terms of pH and size, not necessarily the large, high-pH lakes that produce more and fitter offspring [29].

(iii) Fitness costs of selection

The consequences of traps will depend on which components of fitness are reduced and by how much. In the most extreme case, traps will result in mortality (e.g. [31]), but other non-lethal endpoints such as reduced reproductive success are also possible (e.g. [32]). These various effects may have different consequences for metapopulation growth and persistence (e.g. [33]).

(iv) Species-specific vulnerability to fitness costs

Life-history traits will be an important determinant of an animal’s vulnerability to traps [8,11]. In particular, traits from the ‘slow’ end of the ‘fast–slow continuum’ [34] are likely to increase long-term vulnerability (e.g. delayed sexual maturity, low fecundity and long generation time; see electronic supplementary material, appendix S1). Animals with rapid adaptive potential may be able to respond quickly and escape the effects of traps, while those with low capacity for learning, slow rates of evolution or a lack of behavioural adaptations to change will be most susceptible [11].

We illustrate this framework using a metapopulation modelling approach, and compare how different characteristics of ecological traps can affect metapopulation growth and persistence. As identified above, the impacts of traps will be dependent on a large number of factors. We selected a subset of these, which we predicted *a priori* to be important, and examined how they affected the consequences of traps for metapopulations to evaluate evidence for the following six hypotheses: (i) the effects of traps will be more pronounced when they represent a larger proportion of available habitat; (ii) the chances of an animal encountering a trap will depend on their dispersal ability or perceptual range; (iii) severe (i.e. preferred) traps will reduce metapopulation growth rate and

persistence more than equally preferred traps; (iv) animals that exhibit NHPI will be more likely to select traps; (v) reductions in breeding fitness and mortality will have differential effects; and (vi) animals with life-history traits from the 'slow' end of the fast–slow continuum will be more susceptible to traps.

2. Material and methods

(a) A modelling framework to examine the influence of traps on metapopulations

To accommodate the full range of landscape-, trap- and species-level variation, we used a network-based landscape representation [35] with species-specific attributes (dispersal, fecundity, survival) coupled with a gravity model [36,37] to parametrize habitat selection. Patch attractiveness is a key element determining how a habitat patch will be perceived by an individual, and we implemented this process with a production constraint gravity model [36] of dispersal. With this approach, the functional connectivity between any two habitats is a function of (i) geographical distance, (ii) dispersal capacity, (iii) reproductive output of the source patch, and (iv) size and attractiveness of the destination patch. All metapopulations varied in the number, placement, size and quality of habitat patches containing subpopulations. Species-specific attributes, unique to each metapopulation simulation, included dispersal ability (negative-exponential decay function), perceptual range, habitat preference, survival and fecundity. From this initial landscape, a proportion of habitat patches was selected and converted to traps by decreasing fitness (i.e. survival and/or fecundity) within these patches and increasing their attractiveness ('realized traps'; electronic supplementary material, appendix S2). A natal preference penalty was used to modify the dispersal probability, redistributing individuals to patches with similar qualities. Landscapes often comprised a mosaic of different habitats that vary in location, size and quality [38,39]. When animals have imperfect knowledge of the environment, they can make suboptimal habitat selection decisions [25], resulting in naturally occurring patches with trap-like consequences (e.g. low-quality yet large, and therefore 'attractive', patches). Ecological traps are defined as arising from changes to the attractiveness of and/or preference for a particular habitat [3], so we did not code these trap-like patches (whose attractiveness and/or quality had not been altered) as ecological traps but treated them as natural phenomena of heterogeneous landscapes (electronic supplementary material, appendix S2). However, because the majority of simulations contained trap-like patches, we also evaluated their overall impact on metapopulations (electronic supplementary material, appendix S2). All model parameters are outlined in table 1, and further details of these and the modelling approach more generally are provided in electronic supplementary material, appendices S2–S6.

The consequences of patch-level demographics and animal movement within each metapopulation were quantified by calculating the metapopulation mean lifetime (MMLT) and metapopulation growth rate (λ_M). The network-based MMLT calculation [20,40] accommodates habitat networks consisting of patches of variable size, quality, spacing and a stochastic extinction likelihood, in a computationally efficient approach. Simply, the MMLT is a function of three network characteristics: the dispersal network structure, extinction rates of local populations and the size of habitat patches. We used the Kininmonth *et al.* ([20], eqn 10) approach for calculating MMLT for all metapopulations, using constants for the species-specific minimum patch size coefficient ($\varepsilon = 1.0$), extinction area exponent ($\eta = 0.5$) and the minimum number of immigrants for successful colonization ($\mu = 2.0$). As a result, the patch-level extinction risk in MMLT is a function of its area and quality. Similarly, we used a

metapopulation growth rate calculation sensitive to the spatial structure of the dispersal network, as well as patch-level demographic potential and its contribution to other patches [41]. This network-based λ_M ([41], eqn 13) is dependent on the dispersal network and the individual patch attributes of area, fecundity and survival. The MMLT and λ_M quantify slightly different (extinction risk and growth rate, respectively), yet complementary characteristics of the metapopulation.

To make meaningful comparisons across all models, we quantified the relative impact of traps on λ_M and MMLT by evaluating each metapopulation both with and without ecological traps. These paired models were used to calculate the relative impact of traps on the metapopulation: $\lambda_{M\text{Impact}} = (\lambda_{M\text{Trap}} - \lambda_{M\text{non-Trap}}) / \lambda_{M\text{non-Trap}}$ and $\text{MMLT}_{\text{Impact}} = (\log_{10}(\text{MMLT}_{\text{Trap}} + 1) - \log_{10}(\text{MMLT}_{\text{non-Trap}} + 1)) / \log_{10}(\text{MMLT}_{\text{non-Trap}} + 1)$. Larger negative values in $\lambda_{M\text{Impact}}$ and $\text{MMLT}_{\text{Impact}}$ indicate stronger detrimental consequences of traps on the metapopulation. Owing to the unknown prevalence and strength of NHPI, we analysed each metapopulation pair with and without the natal preference penalty. There was high concordance in metapopulation impact between analyses with and without NHPI, so only results with NHPI are presented.

(b) Model sensitivity analysis

We used a variance-based global sensitivity analysis (SA) framework [42,43] to evaluate the consequences of traps. For computational feasibility, we implemented a non-parametric SA based on a series of meta-models [44–46] using all input parameters (R package CompModSA with 'sensitivity' function). A suite of 3000 parameter combinations generated with a Latin hypercube sample (LHS) scheme [45,47] was used to build each meta-model. Each parameter combination resulted in a unique metapopulation model realization.

Owing to the complexity of the model, expected high-level interactions among parameters and nonlinear responses, we evaluated several meta-models to examine consistency in emergent patterns [45,48,49]: generalized linear model (GLM), quadratic response surface regression (QRS), recursive partitioning regression (TREE) and multi-variate adaptive regression splines (MARS), all implemented in R (GLM with the MASS package, all others with the CompModSA package). These meta-models were chosen as each is expected to perform differently depending on the unknown structure of the response surface (see electronic supplementary material, appendix S2 for meta-model comparisons). For the GLM SA, we calculated the main effects and two-way interactions on the standardized data and visualized the sensitivity of response variables by plotting the effect of one standard deviation change in each parameter on the response [49]. For the non-GLM meta-models, the total sensitivity index, $\hat{T}_j$ [48,50], was used to quantify the relative importance of all input parameters to the relative changes in MMLT and λ_M owing to traps ($\text{MMLT}_{\text{IMPACT}}$ and $\lambda_{M\text{IMPACT}}$, respectively). This index provides a single number summary of the overall importance of each parameter and should be interpreted as the total proportion of the variability in the response surface that is due to each parameter, including all interactions with other parameters [48]. Standard bootstrapping (10 000 samples) was used to create confidence intervals around the mean sensitivity index value.

3. Results

After screening the 3000 unique parameter combinations to remove scenarios where the non-trap metapopulation had a decreasing growth rate ($\lambda_M < 1$) and those lacking realized traps, 2688 (90%) remained. In almost all cases, traps had negative effects on metapopulations in these models (figure 1;

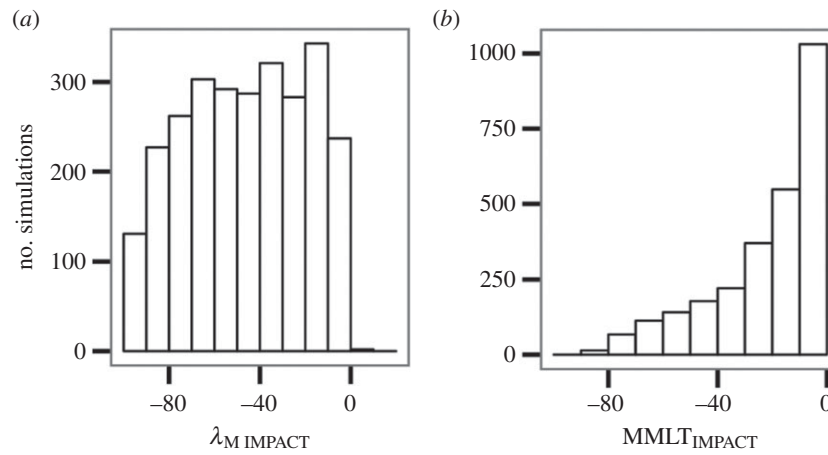


Figure 1. The effects of ecological traps on differences in (a) metapopulation growth rate ($\lambda_{M \text{ IMPACT}}$) and (b) mean metapopulation lifetime ($MMLT_{\text{IMPACT}}$) between trap and non-trap metapopulations ($n = 2688$ simulations).

Table 1. Description of variables included in the model and descriptors of their characteristics. See electronic supplementary material, appendices S2–S6 for further details.

	parameter	description	range
landscape configuration	number habitat patches in landscape (N)	limited to 50 for computational efficiency	[3,50]
	minimum quality of habitat patches (MinQ)	patches were randomly assigned a quality $< \text{MinQ}$	[0,1]
probability of encounter	trap proportion (T.pro)	proportion of patches in the landscape that are traps	[0.1,1]
	dispersal capacity (Disp)	the relative distance at which the probability of dispersal is 0.05; using a negative-exponential function, $p_{ij} = \exp(\theta \times d_{ij})$, where θ is the decay coefficient and d_{ij} is the distance between patches	[0,1]
	perceptual range (Pr)	the perceptual range of a patch is a multiplicative function with patch size, quality and Pr	[0,5]
the likelihood of selection	attractiveness of traps (T.att)	attractiveness of traps is increased by T.att	[1,10]
	preference for natal-like habitats (Np)	dispersal between patches decreases proportional to the difference in quality times Np	[0,1]
the fitness costs of selection	trap survival penalty (T.surv)	survival in traps decreased as $\text{Surv} \times \text{T.surv}$	[0,1]
	trap fecundity penalty (T.fec)	fecundity in traps decreased as $\text{Fec} \times \text{T.fec}$	[0,1]
species-specific vulnerability to these costs	fecundity (Fec)	the number of offspring per unit area as a function of quality: $\text{Fec} \times q_i$	[2,100]
	survival (Surv)	the survival of adults per unit area, as a function of quality: $\text{Surv} \times q_i$	[0,1]

median $\lambda_{M \text{ IMPACT}} = -45.10$, median $MMLT_{\text{IMPACT}} = -14.80$). However, in some rare instances, they were beneficial, resulting in positive $\lambda_{M \text{ IMPACT}}$ values (figure 1).

All criteria in our framework influenced the negative consequences of traps. The proportion of traps (T.pro) in the landscape was a strong influence on both $\lambda_{M \text{ IMPACT}}$ and $MMLT_{\text{IMPACT}}$ (figures 2 and 3), and is likely to be the most important determinant of whether animals encounter traps. We found some evidence to suggest that highly vagile species (i.e. higher Disp) may also be more susceptible to the effects of traps, but perceptual range was less important.

The probability of animals selecting traps is likely to be influenced by their attractiveness relative to other habitats. More dramatic impacts were observed on $\lambda_{M \text{ IMPACT}}$ when the attractiveness of traps (T.att) was higher relative to non-traps. In comparison, trap attractiveness was not important to $MMLT_{\text{IMPACT}}$ (figure 2b). NHPI was not one of the most important factors influencing the consequences of traps, especially for $MMLT_{\text{IMPACT}}$ (Np, figures 2b and 3b). However, our GLM suggested that Np weakened the effects of traps on $\lambda_{M \text{ IMPACT}}$ (figure 3a). When landscapes did not contain traps, Np had only relatively weak effects on $MMLT_{\text{IMPACT}}$.

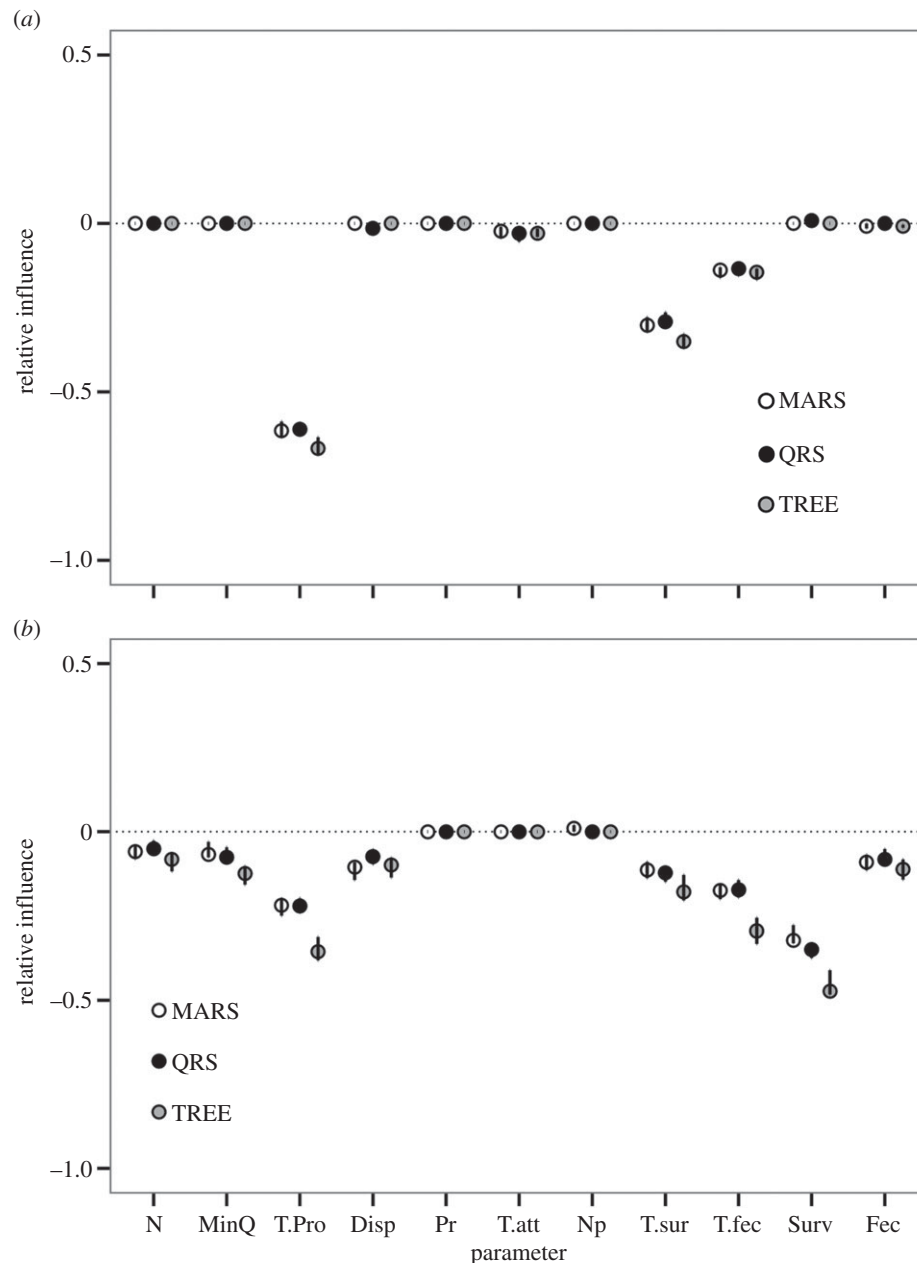


Figure 2. Results of global sensitivity analysis describing the relative influence of variables ($\hat{T}_j$) on differences in metapopulation (a) growth rate ($\lambda_{M\ IMPACT}$) and (b) mean lifetime ($MMLT_{IMPACT}$) between metapopulations with and without ecological traps. Overall fits (R^2) ranged from 0.83 to 0.94 across all models. Negative $\hat{T}_j$ values indicate that as the parameter value increases, the severity of the impact of traps increases (becomes more negative). Model parameters are defined in table 1.

and $\lambda_{M\ IMPACT}$ (figure 4a,b). In comparison, Np generally resulted in stronger positive effects on $\lambda_{M\ IMPACT}$ values when traps were present (figure 4c). We also observed instances, though, where Np magnified the effects of traps on $\lambda_{M\ IMPACT}$ values.

Reductions in fecundity (T.fec) and survival (T.surv) in traps negatively affected both metapopulation responses, and for $MMLT_{IMPACT}$ the magnitude was comparable. However, reduced survival in traps had a stronger negative effect on $\lambda_{M\ IMPACT}$ than reduced fecundity. The positive interaction between the two parameters (T.fec:T.surv; figure 3) reflects the fact that as one parameter increases, the relationship (i.e. slope) between the other parameter and the metapopulation impact increases (or becomes less negative). For example, with a low survival penalty, the relative impact of a high fecundity penalty is quite significant, whereas at high survival penalties, the impact resulting from increasing the fecundity penalty is reduced.

In general, a species's intrinsic survival and fecundity had negative influences on $MMLT_{IMPACT}$ and $\lambda_{M\ IMPACT}$ (Surv and Fec; figures 2 and 3). Model species with higher survival suffered greater (i.e. more negative) metapopulation impacts resulting from ecological traps. Increases in survival and fecundity increased MMLT and λ_M in the absence of traps, but this did not translate into a decreased impact in the presence of traps, as expected. Thus, for a given trap penalty, species with higher fitness will have a greater absolute decrease in reproductive success/survival in trap patches than those species with lower fitness.

4. Discussion

All criteria in our framework significantly influenced the negative consequences of traps, illustrating that assessing

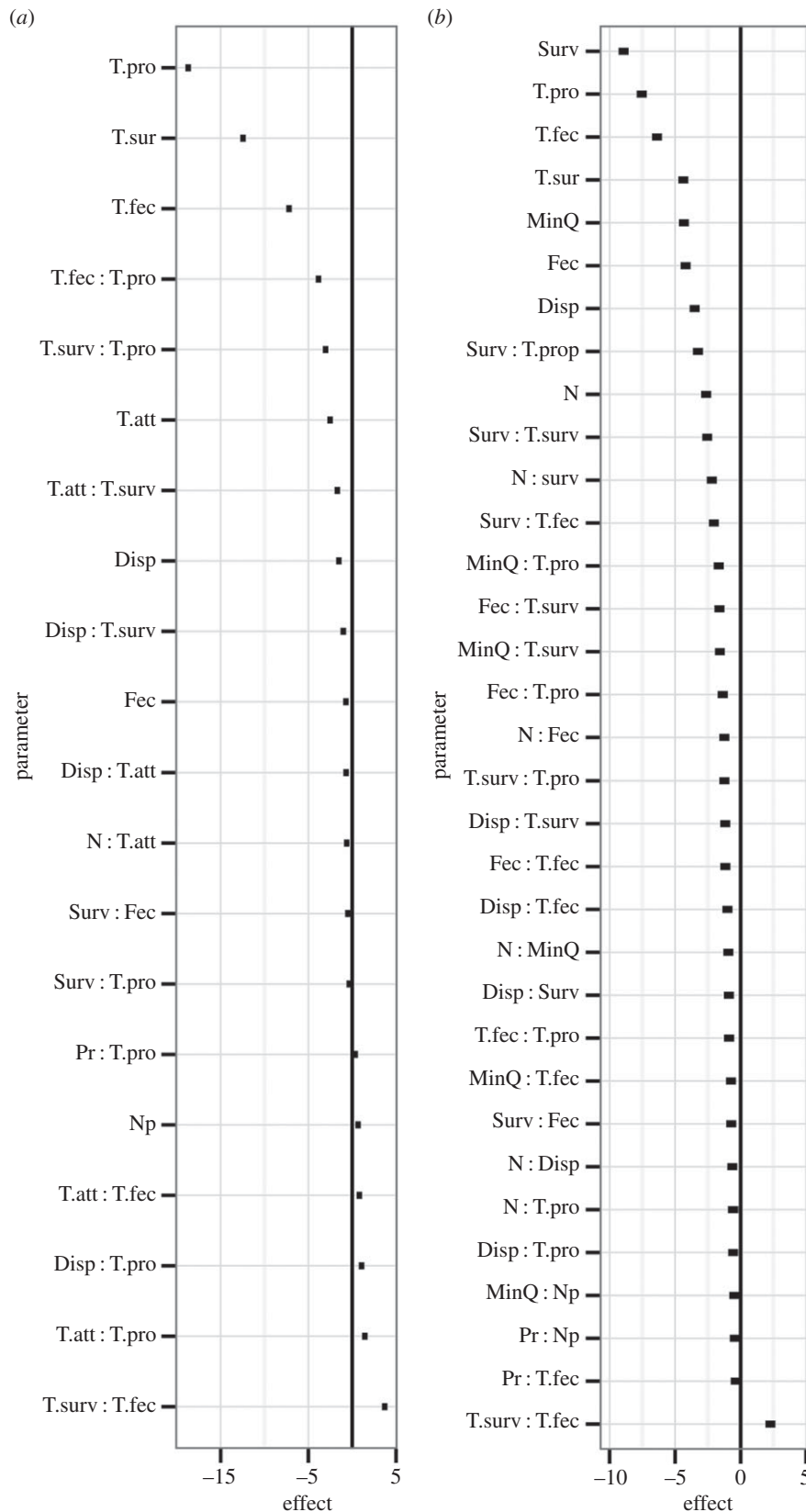


Figure 3. Results of generalized linear model (GLM) describing the relative influence of variables on differences in metapopulation (a) growth rate ($\lambda_{M \text{ IMPACT}}$) and (b) mean lifetime ($MMLT_{\text{IMPACT}}$) between metapopulations with and without ecological traps. Bars show 95% CIs associated with slopes and interactions between slopes. The x-axis describes the effect of a one standard deviation change in each model parameter on the response. Parameters (statistically significant at $p < 0.05$) are organized according to the direction and strength of their influence on the response. Overall fits (R^2) of GLM: (a) 0.91 and (b) 0.77. Model parameters are defined in table 1.

traps requires an approach integrating landscape and movement ecology, habitat selection behaviour, and the life history of animals. We evaluate the evidence below for our six hypotheses to assess their relative influence on the consequences of traps for metapopulation dynamics.

Hypothesis 1. The effects of traps will be more pronounced when they represent a larger proportion of available habitats.

The proportion of traps (T.pro) was a key determinant of how traps reduce both metapopulation growth rate and

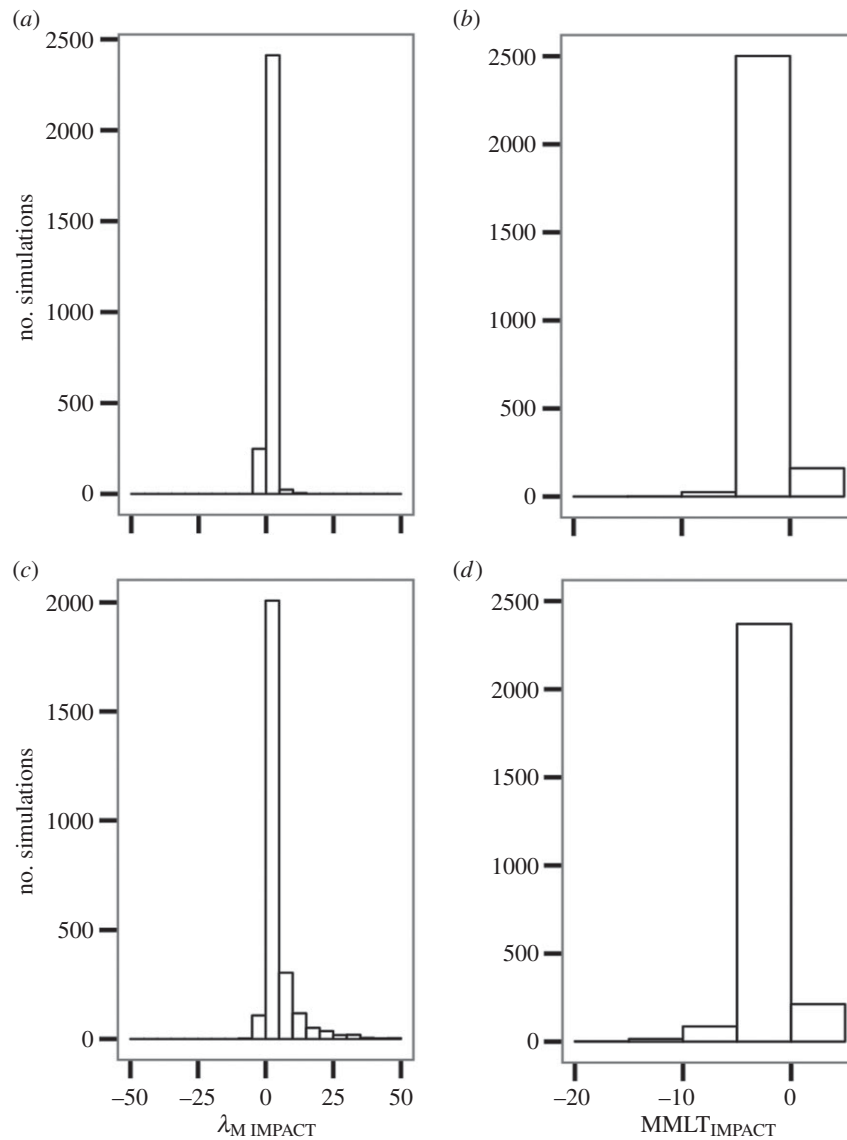


Figure 4. The influence of natal habitat preference induction (NHPI) on metapopulations with and without ecological traps. The four panels illustrate the effects of NHPI on $\lambda_{M \text{ IMPACT}}$ and $MMLT_{\text{IMPACT}}$ when ecological traps (*a,b*) are and (*c,d*) are not present in the landscape. There were 12 simulations where $\lambda_{M \text{ IMPACT}}$ was greater than 50 when traps were present (*c*); these cases are not shown, to allow a clearer presentation of overall results.

mean lifetime. Previous models have suggested there may be a threshold proportion of traps in the landscape above which extinction probability increases, potentially dependent on habitat quality and preferences [9,12]. For example, migratory songbirds are likely to suffer population extirpations when traps represent more than 30% of available habitats [9]. We observed that $\lambda_{M \text{ IMPACT}}$ and $MMLT_{\text{IMPACT}}$ were increasingly negative when T.prop was high, but found no evidence that similar threshold effects occurred when all other habitat attributes (quality, size, placement, etc.) varied continuously across the landscape.

Hypothesis 2. The chances of an animal encountering a trap will depend on their dispersal ability or perceptual range.

Highly dispersive animals may be able to rescue or recolonize patches and thus be less predisposed to extinction risk in fragmented landscapes [51]. Our results illustrate an opposing perspective, with highly vagile species more susceptible to the impact of ecological traps. Our GLM results provide some support for three possible reasons for this

effect: (i) an increased rate of trap encounter (Disp:T.att, Disp:T.pro, figure 3*a*; Disp:T.pro, figure 3*b*), (ii) a greater neighbourhood (i.e. number of habitat patches) that trap patches influence (N:Disp, figure 3*b*) or (iii) a decrease in the local retention of offspring in quality habitat with increased dispersal (see Disp formulation in table 1). The ultimate cause may be a combination of these, in addition to other potential costs of dispersal [52].

While increased perceptual range (Pr) may lower dispersal costs and increase connectivity in fragmented landscapes [53], the opposite has also been shown. For example, simulations studies have shown that animals with no perceptual knowledge of their environment had increased overall metapopulation connectivity in comparison with those with increased cognitive information, at least while energy resources were adequate [54]. We found similar effects, with increased perceptual range having no influence on the impact of traps. The influence of Pr on metapopulation dynamics and the impact of traps may be masked by the randomized spatial structure of our landscapes, which had a strong influence on metapopulation connectivity. On average, the spatial structure of habitat

patches and the species' dispersal potential (Disp) accounted for 84% of the metapopulation connectivity matrix, the remaining proportion determined by the perceptual range, cue distances and attractiveness (gravity) of patches in the model.

Hypothesis 3. Severe (i.e. preferred) traps will reduce metapopulation growth rate and persistence more than equally preferred traps.

Severe traps are likely to lead more frequently and rapidly to the decline and extirpation of animal populations as individuals are attracted away from higher fitness habitats [10,11]. Our results indicate severe traps may similarly have more dramatic consequences than equal-preference traps for metapopulations. In comparison, trap attractiveness was not important to $\text{MMLT}_{\text{IMPACT}}$. This lack of impact was found across all meta-models, suggesting its effects may be somewhat obscured by the strong (and uncontrolled) effect of network topology [20].

Hypothesis 4. Animals that exhibit NHPI will be more likely to select traps.

Our results illustrate that NHPI has a strong influence on habitat selection when traps are present in the landscape, and that generally this resulted in the effects of traps being diluted. Kokko & Sutherland [11] proposed that preferences for natal-like habitat may provide some protection from the effects of traps as the increased productivity of high-quality habitats means that more individuals will be selecting these over poorer-quality options. However, our results also illustrate that NHPI could magnify the effects of traps in some cases (figure 4c). Recent evidence suggests that NHPI does not always lead to the selection of highest-quality habitats (e.g. [29]), and could lead to traps, if for example habitats are exposed to pollutants that go undetected and animals continue to select polluted sites (e.g. bats foraging on non-biting midges associated with sewage effluent [55]). If so, NHPI could, in rare instances, facilitate the initial development of traps and their subsequent persistence through a negative feedback loop where individuals continue to select impacted environments.

Hypothesis 5. Reductions in breeding fitness and mortality will have differential effects.

Studies of traps at the local scale (e.g. those reviewed in [4]) have illustrated how traps may reduce fitness, for example, by characterizing rates of survival or breeding success. Extending this finding to the landscape level, we have modelled how local reductions in fitness affect metapopulation growth and persistence. Our results demonstrate that reduced fecundity (T.fec) or survival (T.sur) in traps resulted in comparable reductions in metapopulation persistence. However, metapopulation growth rate is likely to be more limited when traps reduce survival compared with fecundity. The interaction we observed (T.fec:T.surv) illustrates that when traps reduce one of these elements of fitness, the overall effects are not exacerbated by subsequent reductions in the other.

Hypothesis 6. Animals with life-history traits from the 'fast' end of the fast–slow continuum will be more susceptible to traps.

Our results illustrate that animals with high intrinsic fitness are likely to be more susceptible to the effects of traps, based on having more scope for negative effects to occur. However, species with 'slow' life-history traits will be more likely to suffer local extirpations—high intrinsic fitness may mean that traps can result in larger reductions in fitness, but may also confer increased resilience to traps.

In modelling the consequences of ecological traps on metapopulations, we focused on survival and fecundity to estimate the life-history traits of animals likely to influence their susceptibility to traps. However, other life-history traits (e.g. electronic supplementary material, appendix S1) will probably influence how animals respond once trapped; for example, those traits that facilitate rapid evolution may offer the potential for animals to 'escape' via natural selection for adaptive preferences or existing phenotypic plasticity [11]. Other traits, such as those that influence the evolution of dispersal ability, will potentially also be important. A logical extension to our approach here would be to examine the influence of some of these evolutionary traits on metapopulation growth rate and persistence when traps are present in landscapes.

(a) The triple jeopardy of ecological traps: prevalence, attractiveness and fitness consequences

Complex interactions between the spatial arrangement of traps, their attractiveness and fitness costs, and the life-history traits of animals will ultimately determine how metapopulations respond to traps. However, it is clear that animals are likely to be most at risk when traps occur under the 'triple jeopardy' scenario, whereby they (i) are highly attractive, (ii) result in large reductions in fitness and (iii) represent a large proportion of the available habitat. These observations are intuitive, and similar suggestions have been made about the effects of traps at local scales [11,13], but our study provides the first evidence that they still hold at metapopulation scales.

(b) Ecological traps may be beneficial in rare instances

We present the first evidence that in rare instances, traps may have positive benefits for metapopulations. While traps generally had negative effects, in a small number of situations they increased metapopulation growth rate (positive $\lambda_{\text{M IMPACT}}$). This occurred primarily when traps, characterized by increased attractiveness and only minor fitness costs, served as central stepping stones in a habitat network, effectively increasing landscape-scale connectivity as animals move through the trap patch. This benefit was confirmed through a targeted modelling ensemble. A $19\times$ increase in the likelihood of a positive $\lambda_{\text{M IMPACT}}$ value was achieved by modelling vagile taxa in a high-quality landscape where the proportion of traps was low (less than 30%), the trap attractiveness was high (more than $5\times$) and the fitness consequences were low (penalties < 0.10). We suspect this effect is strongly dependent on the topology of patches and the placement of traps.

(c) The impact of naturally occurring trap-like patches

Our results suggest that trap-like conditions are probably a common phenomenon of metapopulations in landscapes where patches vary in quality and size. More than 87% of simulations contained naturally occurring trap-like patches (electronic supplementary material, appendix S2), and these

represented on average approximately 38% of patches across all simulations. Results from running a targeted global SA with the proportion of natural trap-like patches as a parameter illustrate that while these patches may be common, their effects in the presence of ecological traps are weak (relative influence $\hat{T}_j < 0.03$). With the prevalence of naturally occurring trap-like patches within spatially realistic metapopulations, we suggest clarity is needed in future studies to distinguish between these patches and ecological traps where habitat selection cues and/or habitat quality have been altered.

5. Conclusion

Evaluating the risks ecological traps pose to animal populations requires a greater understanding of their impacts within the landscape. By developing a generalized spatial framework, we have shown that the severity of traps depends not just on their fitness consequences, but also the life-history traits of animals. In particular, traits that increase the likelihood of encountering and selecting traps, as well as a species's vulnerability to the associated fitness costs, are likely to be important. Our findings further demonstrate that the effects of traps become significantly more complicated when the focus is on landscape rather than local scales, requiring a broader consideration of how animals move across spatially heterogeneous landscapes. A crucial

next step to further improve our understanding is to use our findings to develop and test predictions about the effects of traps on metapopulations in the field.

Ecological traps are likely to become increasingly common as humans continue to dramatically alter the landscape, and therefore have important implications for the management of animal populations worldwide. Incorporating traps into management and conservation practices will require close tracking of changes in both 'real' and perceived habitat quality over time, and a greater consideration of animal behaviour [4]. At the local scale, either increasing the quality or decreasing the attractiveness of traps will reduce their effects on animals, but, as our study highlights, managing their effects at the landscape scale is likely to be significantly more complex. Habitats need to be managed within the context of landscape mosaics and the entire landscape [56], rather than at the scale of habitat patches. There is an urgent need, therefore, to assess how traps fit within the gradients of habitat quality that occur in the face of anthropogenic disturbances to the landscape, and to use this broader perspective as the basis for minimizing their effects on animal populations.

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Reference

- Sih A. 2013 Understanding variation in behavioural responses to human-induced rapid environmental change: an overview. *Anim. Behav.* **85**, 1077–1088. (doi:10.1016/j.anbehav.2013.02.017)
- Schlaepfer MA, Runge MC, Sherman PW. 2002 Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**, 474–480. (doi:10.1016/S0169-5347(02)02580-6)
- Robertson BA, Hutto RL. 2006 A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* **87**, 1075–1085. (doi:10.1890/0012-9658(2006)87[1075:affuet]2.0.co;2)
- Robertson BA, Rehege JS, Sih A. 2013 Ecological novelty and the emergence of evolutionary traps. *Trends Ecol. Evol.* **28**, 552–560. (doi:10.1016/j.tree.2013.04.004)
- Dwernychuk LW, Boag DA. 1972 Ducks nesting in association with gulls—an ecological trap? *Can. J. Zool.* **50**, 559–563. (doi:10.1139/z72-076)
- Kriska G, Horvath G, Andrikovics S. 1998 Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *J. Exp. Biol.* **201**, 2273–2286.
- Hollander FA, Van Dyck H, San Martin G, Titeux N. 2011 Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *PLoS ONE* **6**, e25703. (doi:10.1371/journal.pone.0025703)
- Battin J. 2004 When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* **18**, 1482–1491. (doi:10.1111/j.1523-1739.2004.00417.x)
- Donovan TM, Thompson FR. 2001 Modelling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecol. Appl.* **11**, 871–882. (doi:10.1890/1051-0761(2001)011[0871:mtetha]2.0.co;2)
- Fletcher RJ, Orrock JL, Robertson BA. 2012 How the type of anthropogenic change alters the consequences of ecological traps. *Proc. R. Soc. B* **279**, 2546–2552. (doi:10.1098/rspb.2012.0139)
- Kokko H, Sutherland WJ. 2001 Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evol. Ecol. Res.* **3**, 537–551.
- Delibes M, Gaona P, Ferreras P. 2001 Effects of an attractive sink leading into maladaptive habitat selection. *Am. Nat.* **158**, 277–285. (doi:10.1086/321319)
- Kristan WB. 2003 The role of habitat selection behavior in population dynamics: source–sink systems and ecological traps. *Oikos* **103**, 457–468. (doi:10.1034/j.1600-0706.2003.12192.x)
- Whittingham MJ, Wilson JD, Donald PF. 2003 Do habitat association models have any generality? Predicting skylark *Alauda arvensis* abundance in different regions of southern England. *Ecography* **26**, 521–531. (doi:10.1034/j.1600-0587.2003.03522.x)
- Hanski I, Gaggiotti OE. 2004 *Ecology, genetics, and evolution of metapopulations*. Burlington, MA: Elsevier Academic Press.
- Franken RJ, Hik DS. 2004 Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *J. Anim. Ecol.* **73**, 889–896. (doi:10.1111/j.0021-8790.2004.00865.x)
- Kindvall O. 1996 Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology* **77**, 207–214. (doi:10.2307/2265670)
- Dias PC. 1996 Sources and sinks in population biology. *Trends Ecol. Evol.* **11**, 326–330. (doi:10.1016/0169-5347(96)10037-9)
- Pulliam HR. 1988 Sources, sinks, and population regulation. *Am. Nat.* **132**, 652–661. (doi:10.1086/284880)
- Kininmonth S, Drechsler M, Johst K, Possingham HP. 2010 Metapopulation mean life time within complex networks. *Mar. Ecol. Prog. Ser.* **417**, 139–149. (doi:10.3354/meps08779)
- Fletcher RJ, Revell A, Reichert BE, Kitchens WM, Dixon JD, Austin JD. 2013 Network modularity reveals critical scales for connectivity in ecology and evolution. *Nat. Commun.* **4**, 1–7. (doi:10.1038/ncomms3572)
- Brown JH, Kodric-Brown A. 1977 Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**, 445–449. (doi:10.2307/1935620)
- Resetarits Jr W, Binkley C. 2013 Patch quality and context, but not patch number, drive multi-scale colonization dynamics in experimental aquatic

- landscapes. *Oecologia* **173**, 933–946. (doi:10.1007/s00442-013-2644-5)
24. Serrano D, Tella JL. 2003 Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. *J. Anim. Ecol.* **72**, 400–410. (doi:10.1046/j.1365-2656.2003.00707.x)
 25. Lima S, Zollner PA. 1996 Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* **11**, 131–135. (doi:10.1016/0169-5347(96)81094-9)
 26. Huijbers CM, Nagelkerken I, Loo de, Schulten IE, Siegenthaler A, Holderied MW, Simpson SD. 2012 A test of the senses: fish select novel habitats by responding to multiple cues. *Ecology* **93**, 46–55. (doi:10.1890/10-2236.1)
 27. Davis JM. 2008 Patterns of variation in the influence of natal experience on habitat choice. *The Q. Rev. Biol.* **83**, 363–379. (doi:10.1086/592851)
 28. Burgess SC, Treml EA, Marshall DJ. 2012 How do dispersal costs and habitat selection influence realized population connectivity? *Ecology* **93**, 1378–1387. (doi:10.1890/11-1656.1)
 29. Piper WH, Palmer MW, Banfield N, Meyer MW. 2013 Can settlement in natal-like habitat explain maladaptive habitat selection? *Proc. R. Soc. B* **280**, 20130979. (doi:10.1098/rspb.2013.0979)
 30. Davis JM, Stamps JA. 2004 The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* **19**, 411–416. (doi:10.1016/j.tree.2004.04.006)
 31. Horvath G, Bernath B, Molnar G. 1998 Dragonflies find crude oil visually more attractive than water: multiple-choice experiments on dragonfly polarotaxis. *Naturwissenschaften* **85**, 292–297. (doi:10.1007/s001140050503)
 32. Weldon AJ, Haddad NM. 2005 The effects of patch shape on indigo buntings: evidence for an ecological trap. *Ecology* **28**, 1422–1431. (doi:10.1890/04-0913)
 33. Bossuyt B, Honnay O. 2006 Interactions between plant life span, seed dispersal capacity and fecundity determine metapopulation viability in a dynamic landscape. *Landscape Ecol.* **21**, 1195–1205. (doi:10.1007/s10980-006-0016-9)
 34. Reynolds JD. 2003 Life histories and extinction risk. In *Macroecology: concepts and consequences* (eds TM Blackburn, KJ Gaston), pp. 195–217. Oxford, UK: Blackwell.
 35. Urban DL, Minor ES, Treml EA, Schick RS. 2009 Graph models of habitat mosaics. *Ecol. Lett.* **12**, 260–273. (doi:10.1111/j.1461-0248.2008.01271.x)
 36. Muirhead J, Madsaas H. 2011 Evaluation of stochastic gravity model selection for use in estimating non-indigenous species dispersal and establishment. *Biol. Invasions* **13**, 2445–2458. (doi:10.1007/s10530-011-0070-3)
 37. Roy JR, Thill J-C. 2003 Spatial interaction modelling. *Papers Reg. Sci.* **83**, 339–361. (doi:10.1007/s10110-003-0189-4)
 38. Hanski I, Ovaskainen O. 2000 The metapopulation capacity of a fragmented landscape. *Nature* **404**, 755–758. (doi:10.1038/35008063)
 39. Day JR, Possingham HP. 1995 A stochastic metapopulation model with variability in patch size and position. *Theor. Popul. Biol.* **48**, 333–360. (doi:10.1006/tpbi.1995.1034)
 40. Drechsler M. 2009 Predicting metapopulation lifetime from macroscopic network properties. *Math. Biosci.* **218**, 59–71. (doi:10.1016/j.mbs.2008.12.004)
 41. Figueira WF, Crowder LB. 2006 Defining patch contribution in source-sink metapopulations: the importance of including dispersal and its relevance to marine systems. *Popul. Ecol.* **48**, 215–224. (doi:10.1007/s10144-006-0265-0)
 42. Sobol IM. 2001 Global sensitivity indices for nonlinear mathematical models and their Monte Carlo estimates. *Math. Comput. Simul.* **55**, 271–280. (doi:10.1016/S0378-4754(00)00270-6)
 43. Cariboni J, Gatelli D, Liska R, Saltelli A. 2007 The role of sensitivity analysis in ecological modelling. *Ecol. Model.* **203**, 167–182. (doi:10.1016/j.ecolmodel.2005.10.045)
 44. Friedman JH. 2001 Greedy function approximation: a gradient boosting machine. *Ann. Stat.* **29**, 1189–1232. (doi:10.1214/aos/1013203451)
 45. De'ath G. 2007 Boosted trees for ecological modeling and prediction. *Ecology* **88**, 243–251. (doi:10.1890/0012-9658(2007)88[243:BTFEMA]2.0.CO;2)
 46. Makler-Pick V, Gal G, Gorfine M, Hipsey MR, Carmel Y. 2011 Sensitivity analysis for complex ecological models—a new approach. *Environ. Model. Softw.* **26**, 124–134. (doi:10.1016/j.envsoft.2010.06.010)
 47. Helton JC, Davis FJ. 2003 Latin hypercube sampling and the propagation of uncertainty in analyses of complex systems. *Reliab. Eng. Syst. Safety* **81**, 23–69. (doi:10.1016/S0951-8320(03)00058-9)
 48. Storlie CB, Swiler LP, Helton JC, Sallaberry CJ. 2009 Implementation and evaluation of nonparametric regression procedures for sensitivity analysis of computationally demanding models. *Reliab. Eng. Syst. Safety* **94**, 1735–1763. (doi:10.1016/j.res.2009.05.007)
 49. Coutts S, Yokomizo H. 2014 Meta-models as a straightforward approach to the sensitivity analysis of complex models. *Popul. Ecol.* **56**, 7–19. (doi:10.1007/s10144-013-0422-1)
 50. Homma T, Saltelli A. 1996 Importance measures in global sensitivity analysis of nonlinear models. *Reliab. Eng. Syst. Safety* **52**, 1–17. (doi:10.1016/0951-8320(96)00002-6)
 51. Henle K, Davies K, Kleyer M, Margules C, Settele J. 2004 Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.* **13**, 207–251. (doi:10.1023/B:BIOC.0000004319.91643.9e)
 52. Bonte D *et al.* 2012 Costs of dispersal. *Biol. Rev.* **87**, 290–312. (doi:10.1111/j.1469-185X.2011.00201.x)
 53. Öckinger E, Van Dyck H. 2012 Landscape structure shapes habitat finding ability in a butterfly. *PLoS ONE* **7**, e41517. (doi:10.1371/journal.pone.0041517)
 54. Vuilleumier S, Perrin N. 2006 Effects of cognitive abilities on metapopulation connectivity. *Oikos* **113**, 139–147. (doi:10.1111/j.0030-1299.2006.14405.x)
 55. Abbott IM, Sleeman DP, Harrison S. 2009 Bat activity affected by sewage effluent in Irish rivers. *Biol. Conserv.* **142**, 2904–2914. (doi:10.1016/j.biocon.2009.07.012)
 56. Lindenmayer D *et al.* 2008 A checklist for ecological management of landscapes for conservation. *Ecol. Lett.* **11**, 78–91. (doi:10.1111/j.1461-0248.2007.01114.x)

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Population status of the South Rockies and Flathead grizzly bear populations in British Columbia, 2006-2014

11 May 2016



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SUMMARY

South Rockies Grizzly Bear Population

- The grizzly bear population north of Highway 3 in the Elk, Bull and White river valleys of southeastern British Columbia (BC) declined about 40% between 2006 and 2013.
- Hunting was closed in the population unit during 2011 and 2012 and opened during 2013 with fewer licences and lower quotas than were issued during 2006-2010.
- Mortality rates roughly doubled between 2006 and 2013 as the population declined.
- There is a need to reduce mortality of grizzly bears in the South Rockies population unit.

Flathead Grizzly Bear Population

- South of Highway 3, in the Flathead valley, the population declined between 2007 and 2010 and increased from 2010 to 2014.
- This population trend aligned with the more demographic analysis by McLellan (2015) in the southeast portion of this unit, which suggests the decline McLellan (2015) observed was geographically broader than his study area.

Conclusions

- The higher female mortality rate in the South Rockies, compared to the Flathead valley, was likely the proximate reason for the different population trajectories in these two adjacent areas.
- As in the Flathead, the population decline in the South Rockies was probably precipitated by a decade of poor forage production which occurred during a series of summers that were unusually dry compared to the previous two decades.
- The combination of forage failure and increased human-caused mortality caused a decline in grizzly bear numbers in the South Rockies unit which will require 5 to 10 years to recover.
- We suspect the actual number of bears killed in the South Rockies was greater than was recorded in the Compulsory Inspection data and, the methods of accounting for the unreported mortalities used by the province underestimated unrecorded human-caused mortality during the period of population decline.
- In the South Rockies, the number of unrecorded kills must have been several times larger than the recorded non-hunter kills to obtain the population trend we observed. The magnitude and cause of unreported mortality should be further investigated.

INTRODUCTION

The South Rockies is one of three Grizzly Bear Population Units (GBPUs) in British Columbia with consistently high levels of human-caused grizzly mortality ([Artelle et al. 2013](#)). Managers have reduced hunting opportunities in this unit many times because mortality rates exceeded targets while local residents argued that grizzly bear numbers were high. Ongoing uncertainty regarding population trend and sustainable kill levels has made managing the grizzly bear harvest in this portion of BC complex and controversial.

The grizzly bear population in the southern Rocky Mountains of BC and Alberta are integral to the connectivity of this species within its North American range (Fig. 1). This population connects the grizzly bear population further south, in the Northern Continental Divide Ecosystem of Montana with the continuous population to the north. Areas to the east and west of the BC and Alberta Rocky Mountain populations are unoccupied by grizzly bears (Fig. 1; [Proctor et al. 2012](#)), highlighting the continental significance of the Rocky Mountain populations. However, connectivity within the southern Rocky Mountain populations is hindered by linear human development in valley bottoms ([Proctor et al. 2015](#), [Lamb et al. In Review](#)) where high mortality rates limit connectivity between populations on either side of the valleys. The corridor along Highway 3 has much greater development than any other corridor through the Canadian Rocky Mountains and is the main connectivity fracture for grizzly bear populations the Rocky Mountains.

Much of the non-hunting grizzly mortality in this area occurs in the Highway 3 corridor, where human settlement and other development occurs in close proximity to very good bear habitat in the surrounding mountains. This mortality has reduced bear density near the corridor and produced a “sink” scenario resulting in a net immigration into the corridor from the adjacent South Rockies and Flathead areas ([Lamb et al. In Review](#)). This flow of bears into the corridor means that “sink” areas of high mortality can influence the population dynamics of adjacent “source” areas tens of kilometers away by attracting immigrants into the mortality area.

Population density in the South Rockies in 2006 was similar to that measured in the 1990s, while the density in the Flathead unit had likely declined since the mid-1990s ([Mowat et al. 2013a](#)). [McLellan \(2015\)](#) found the grizzly bear population in the southeast corner of the Flathead GBPU rapidly increased in the 1980s and 1990s but then declined during the 2000s. He suggested the period of increase was a result of high historic mortality causing low densities prior to the 1970s coupled with reducing mortality beginning in the late 1960s and 1970s, due to more restrictive hunting regulations and increased general concern over the status of grizzly bears. The decline period was related to the high density of bears combined with greatly reduced huckleberry production from 1998 to 2008. A similar reduction in huckleberry production was documented in the Cabinet Mountains, 130 km west of the Flathead ([Holden et al. 2012](#)). [McLellan \(2015\)](#) is one

of the few demonstrations of food limitation directly influencing demography for a grizzly bear population.

In response to ongoing conservation and management concerns, population monitoring began in the South Rockies in 2006 and in the Flathead unit in 2009. The intent was to build on earlier genetic databases to assess past demography and monitor population trend into the future. The objectives of this report are to determine recent population growth rates and annual abundance for the South Rockies and Flathead GBPU's. We then use annual estimates of abundance and mortality records to calculate mortality rates by cause (road/rail, hunting, control and illegal kills) and sex to inform population management decisions.

STUDY AREA

The study area covers roughly 12,000 km² of the southern Canadian Rocky Mountains (Fig. 1). Portions of this area in the east have very high quality habitat for grizzly bears, while there are areas of low quality habitat in the west. This area comprises two of the grizzly bear population units in the Kootenay Region, the Flathead (3434 km²) and the South Rockies (8303 km²). GBPU's are the spatial basis for population management across the province (see <http://www.env.gov.bc.ca/wld/grzz/>). The southern border of the study area is the Canada-United States boundary. The population has been increasing recently south of the international boundary adjacent to the Flathead unit (Mace et al. 2012). The western border is the Rocky Mountain Trench, which does not support year-round grizzly bear populations. The eastern boundary is the BC-Alberta border, and the northern boundary is where the headwaters of the Elk and White rivers meet those of the Kootenay and Palliser rivers to the north. In 2014 we discontinued sampling in the Bull and White rivers for logistical reasons.

Most human settlement in the study area occurs in the East Kootenay Trench and along the lower Elk river. Development varies from ski resorts at Fernie to five large coal mines north and south of Sparwood which are concentrated on large tracts of private lands. Logging occurs throughout the study area and, while agriculture is common, it occurs mostly along the western boundary. The east fork of the Elk river valley joins the Crowsnest Pass and provides a low elevation pass through the Rocky Mountains. A major highway (Hwy 3) and railroad (Canadian Pacific Railroad) occur here and these developments, along with the linear human settlement found in the corridor, affect grizzly bear habitat use, mortality, and movement.

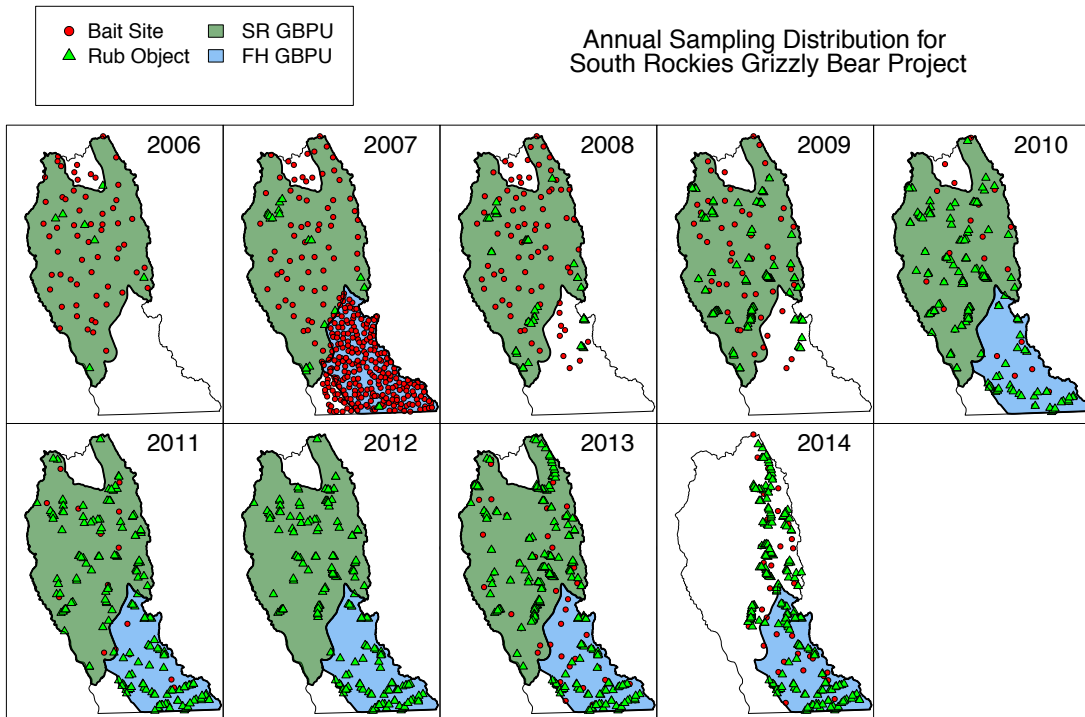
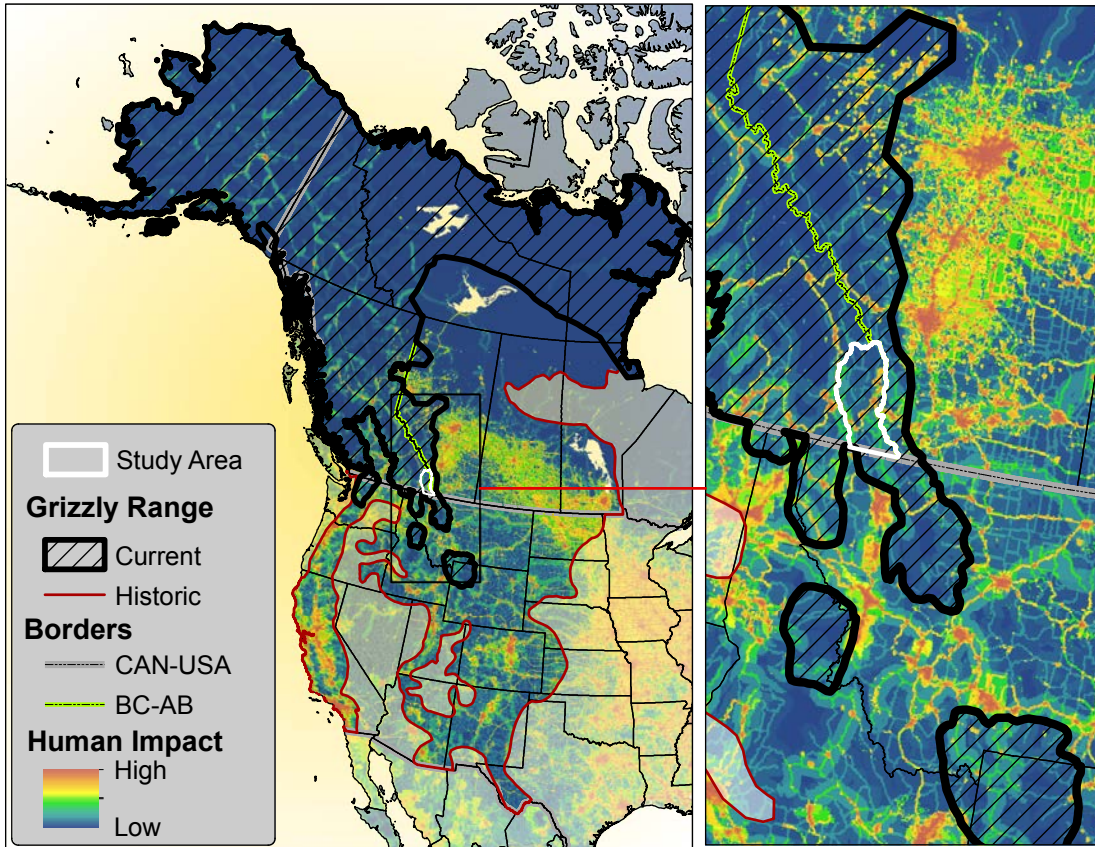


Fig. 1. TOP: Current and historic distribution of grizzly bears across North America with NASA human impact index underlain and study area boundary in white. Our study area is a key connectivity corridor along the spine of the Rocky Mountains. BOTTOM: Annual sampling distribution for the South Rockies and Flathead GBPU. When a unit is white, it indicates that there was incomplete sampling coverage in that year and these data were not used in the analysis. Temporal gaps in sampling were accommodated by adjusting the time intervals in the analysis.

METHODS

We used data from an ongoing population inventory of the South Rockies and Flathead grizzly bear population units (Mowat et al. 2013a) and from a single-year inventory done in the Flathead in 2007 (Grizzly Bear Study Team 2008). Mortality data came from the Compulsory Inspection (CI) database which is managed by the BC Ministry of Forests, Lands and Natural Resource Operations. Field and lab methods were described in detail by Mowat et al. (2013a). Briefly, we used standard bait site and rub tree methods to remove hair from bears and standard methods to genotype individuals to assign individual identity and gender. We attempted to space sampling evenly across the study area although access affected local effort. Annual trapping effort was roughly one fourth of what has been used previously to generate population estimates using closed mark-recapture models (Mowat et al. 2005, Kendall et al. 2009) and varied considerably among years.

Table 1. Annual capture results for the South Rockies GBPU (2006-2013) using bait sites and rub trees to remove hair and microsatellite profiling to identify individuals.

Year	Bait Sites	Rub Trees	Trap Nights	Start	End	Individuals Detected	Males	Females
2006	63	6	1933	Jun-11	Jul-29	78	35	43
2007	72	20	2361	Jun-12	Jul-21	87	37	50
2008	66	34	2595	Jun-14	Sep-20	76	35	41
2009	50	110	6487	Jun-23	Sep-25	110	61	49
2010	17	132	8569	May-26	Oct-30	66	37	29
2011	14	99	9959	Jun-17	Oct-19	66	39	27
2012	0	116	12116	Jun-05	Oct-18	68	41	27
2013	34	160	15173	Jun-27	Oct-10	107	49	58

Table 2. Annual capture results for the Flathead GBPU using bait sites and rub trees to remove hair and microsatellite profiling to identify individuals.

Year	Bait Sites	Rub Trees	Trap Nights	Start	End	Individuals Detected	Males	Females
2007 ^a	230	0	3141	May-31	Jul-29	80	31	49
2010	8	45	4245	Jun-22	Oct-28	21	13	8
2011	8	83	8129	Jun-16	Oct-07	32	23	9
2012	0	84	9536	Jun-22	Oct-15	42	25	17
2013	18	81	9273	Jun-12	Oct-11	38	21	17
2014	20	104	14011	May-22	Oct-12	69	34	35

^a sites were moved every session so each site was only used for < 2 weeks.

Demographic analyses

Individual capture histories were constructed for each GBPU and analyzed using a Pradel robust design model (PRDM) implemented in Program MARK ([White and Burnham 1999](#)) and the RMark package (Laake 2013) in the statistical software R. A capture history is the coded detection data for each bear detected in the study and is a standard form to input data for mark-recapture analysis. The PRDM is a combination of the Pradel estimator ([Pradel 1996](#)), which estimates demographic parameters of open populations ([Nichols and Hines 2002](#)) and, the Huggins formulation of the closed population design, used to estimate detection success and population size ([Huggins 1991](#)). The robust design is based on multiple primary sampling sessions (years in our case) within which multiple secondary sessions are nested (2-4 week trapping sessions in our case; [Gardner et al. 2010](#)). The annual capture histories for each GBPU comprised two bait site and one rub tree session per year, except in 2012, when we only deployed rub trees and had four secondary sessions. We split rub trees and bait sites into separate sessions as these traps are known to have different capture probabilities ([Boulanger et al. 2008](#), [Lamb et al. In Press](#)).

We tested models of capture probability as a function of six covariates: 1) sex, 2) trap type [bait site or rub tree], 3) effort [by trap nights, which is the total number of nights a trap type was set each secondary session], 4) year [2006-2014], 5) season [secondary session] and, 6) project [for the Flathead, where slightly different bait site methods were used in 2007]. We used Akaike's Information Criterion corrected for small sample size (AICc, [Lebreton and Burnham 1992](#); [Anderson and Burnham 2002](#)) to select a top model.

We used the top model to estimate apparent survival (ϕ), apparent recruitment (f), realized population growth (λ), annual abundance (N), and the probability of capture (p ; which is a nuisance parameter in this study) for each GBPU. The PRDM model estimates "apparent" survival because mortality cannot be distinguished from emigration because in both cases the bear is never

recaptured in the population. Similarly, “apparent” recruitment is estimated because detection of a new individual within the study area is indistinguishable from the detection of an individual moving into the study area. The resulting measure of realized population growth is the sum of the probability of entering the population (apparent recruitment) and the probability of remaining in the population (apparent survival; Nichols and Hines 2002).

Pradel assumptions

The main assumptions of the PRDM are: 1) the area being sampled does not change through time, 2) animals must have a non-zero chance of being detected some time during the study and, 3) the population is closed during secondary sampling sessions (sampling conducted within each year) but can be open to births, deaths and movements between primary sessions (between years).

To ensure these data conformed to model assumptions:

1) We reduced the sampling area for each GBPU to the minimum area of continuous annual sampling, which necessitated the removal of the North White river, Quarry and Cadorna Creeks in the South Rockies, and the Galton Range in the Flathead. We did not sample each study area in all years of sampling (Fig. 1, Tables 1-2), but this was accommodated by amending the time intervals of sampling.

2) We have no reason to believe that any animals in the study had zero probability of capture. Recent evidence has shown that all subsets of the grizzly bear population are susceptible to bait sites ([Kendall et al. 2009](#)) and rub trees ([Clapham et al. 2012](#)). Furthermore, we sampled each region for 6 (Flathead) and 8 years (South Rockies), allowing for broad spatial coverage of the region and many opportunities for individual bears to be captured.

3) We believe our study areas were largely demographically closed during sampling because females with cubs emerge from the den much earlier than the beginning of our sampling ([Haroldson et al. 2002](#)), and the majority of human-caused bear mortalities occurred outside our sampling period (Fig. A5). In addition, juveniles are the primary dispersers and most juvenile dispersal ([McLellan and Hovey 2001](#); [Proctor and McLellan 2004](#); [Støen et al. 2006](#)) also occurs before or after our sampling efforts ([Elfström et al. 2014](#)), reducing the risk of bias due to movement in or out of the study areas.

Human-caused mortality rates

We used annual abundance estimates and the mortality data to calculate observed total and sex-specific human-caused mortality rates. In BC, annual sex-specific mortality targets are calculated using the total population estimate because population estimates for each sex are rarely available. Population estimates are multiplied by the desired harvest rate to generate the annual mortality

target though mortality is managed over a five year interval. The number of resident hunting tags awarded each year is based on the past hunting success in each hunting unit. The number of tags awarded always exceeds the mortality target because hunter success is never 100%. We also present sex-specific kill rates based on the population estimate for each sex because they better index the effect of mortality on population growth, though we recognize that population managers do not routinely have this information available. Although all legal hunter harvests and many non-hunting mortalities are recorded in the mortality data, some human-caused mortalities go unrecorded. We used two methods to account for unreported mortality: 1) 2% of the total population (which implies 1% of the female population), which was calculated using a model and is used by BC grizzly bear population managers to account for unreported mortality in all GBPU (referred to as the “policy-based method”) and, 2) a value equal to the reported non-hunter mortality (thus, estimated total non-hunting mortality = reported non-hunting mortality * 2, and estimated unreported mortality = reported non-hunting mortality), which was roughly equivalent to the results of a meta-analysis of mortality of radio-collared grizzly bears that included data from the southern Flathead valley ([McLellan et al. 1999](#)). We refer to this method as the “data-based method”. In this report we present results from the data-based method because we felt it was a better index of actual mortality. Results from the policy-based method are included in the Appendix for comparison.

All statistical analysis were done using the open source programs MARK and R and error bars show standard errors in all figures.

RESULTS

Mortality data

Between 2006 and 2014, there were 116 grizzly bear mortalities recorded in the South Rockies and 44 in the Flathead (Fig. 2). In the Flathead, hunting was the main cause of human-caused deaths while hunting kills accounted for roughly one third of all kills in the South Rockies (Fig. 4). Of the human-caused mortalities in the South Rockies, 38% were hunter kills, 25% were for animal control and other similar reasons, 28% occurred on highways and railways and 8% were illegal. In the Flathead, 91% of recorded kills were by hunters and 9% were control kills. Hunting kills fluctuated annually due to changes in opportunity and success. There were four years when the season was partly or completely closed in the South Rockies while there were no closures during our period of study (2006-2014) in the Flathead. On average, the number of hunting kills declined during the study in the South Rockies while there was little change in the Flathead. The number of hunting kills has been declining slowly since the 1990s in southeast BC. Conversely, recorded non-hunting mortality has been increasing regionally and provincially since the 1980s. There were very

few rail and road kills recorded in the 1980s and 1990s, but this source of mortality increased dramatically in southeast BC beginning in 2000.

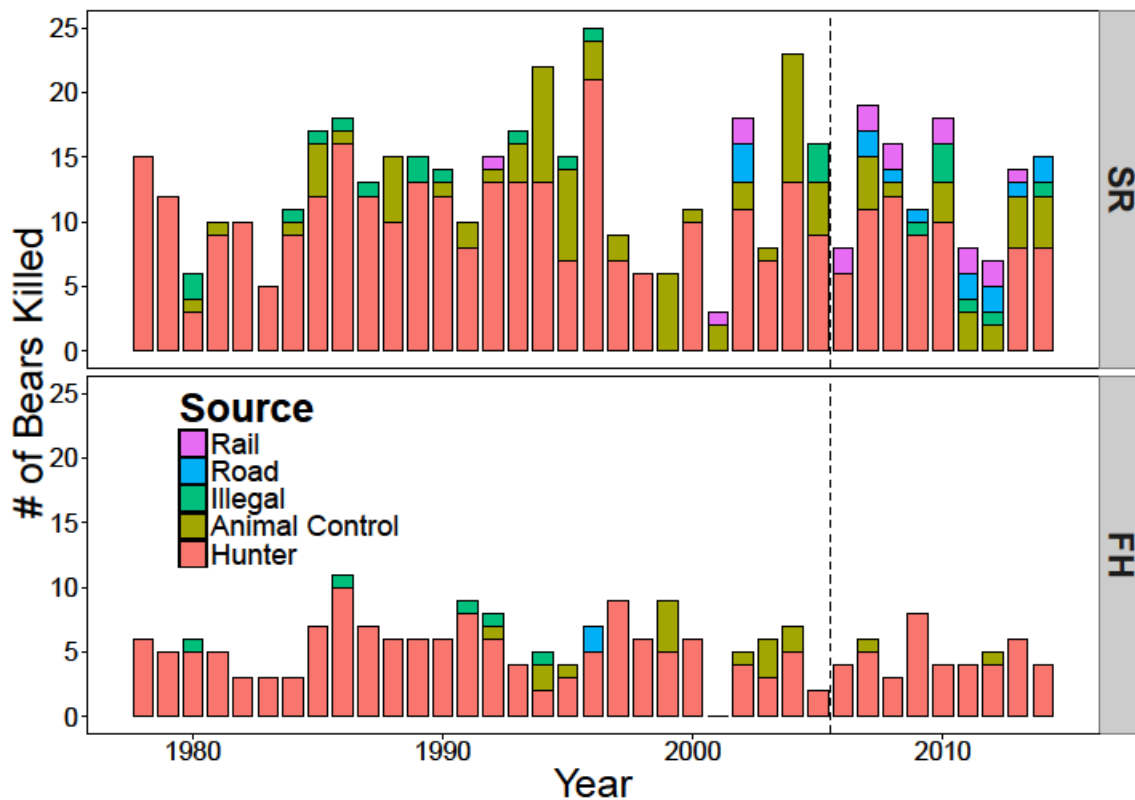


Fig. 2. Recorded grizzly bear mortalities in the South Rockies (SR) and Flathead (FH) population units from 1978-2014 by cause of death. The vertical dotted line denotes the beginning of this study (2006). Road and rail mortalities were not specifically recorded before 2002 and some may have been lumped into the control kills category.

Field sample effort and success

Sample coverage in the South Rockies was continuous from 2006 to 2013; however, effort shifted from largely bait sites to largely rub trees until 2013 when bait site effort increased (Table 1). Bait site effort was more evenly spaced than rub tree effort, but an area in the north was rarely sampled by either method in later years (Fig. 1). The Flathead was first sampled in 2007 and this effort was intensive and used only baited sites that were moved each session (Table 2). The entire area was not sampled again until 2010 and, most of the effort following 2007 was using rub trees until 2013 (Fig. 1). In the South Rockies we detected between 66 and 110 grizzly bears each year, while in the Flathead we detected between 21 and 80 bears each year (Tables 1 & 2). More males were detected at rub trees than females and, the proportion of recaptures of males at rub trees

was 2-3 times that of females (Table 3). Conversely, more females than males were captured at baited sites (Table 3).

Table 3. Trap effort and capture information of individual grizzly bears by sex and trap type for the South Rockies and Flathead GBPU with all data 2006 to 2014 pooled. The marked column tallies the number of bears initially marked with each method, and the recap column tallies the number of individual bear-capture events following their initial capture. The recapture proportion is the number of bear-capture events relative to the initial detection for each sex and trap type.

GBPU	Sex	Individuals	Trap	Site Checks	Marked	Recap	Recapture Proportion
SR GBPU	Total	351	Bait Site	594	261	170	0.65
			Rub Tree	1779	187	251	1.34
	Female	189	Bait Site	594	144	88	0.61
			Rub Tree	1779	87	64	0.74
FH GBPU	Male	162	Bait Site	594	117	82	0.7
			Rub Tree	1779	100	187	1.87
	Total	192	Bait Site	337	121	66	0.55
			Rub Tree	1420	109	130	1.19
	Female	99	Bait Site	337	71	45	0.63
			Rub Tree	1420	46	21	0.46
	Male	93	Bait Site	337	50	21	0.42
			Rub Tree	1420	63	109	1.73

Population analysis

Covariates that best explained variations in capture probably in the capture-recapture model were similar between units and to previous work on this species (Boulanger et al. 2008). The most supported model in both units included the sex of the bear, the type of trap used (rub tree or bait site), an interaction between sex and trap type, trapping effort, secondary session, and year of sampling. This model had a weight of 1 in the South Rockies and 0.75 in the Flathead.

The population trend was consistently negative in the south Rockies during 2006-2013, while in the Flathead the population trend was negative during 2007-2010 and then increased from 2010-2014 (Fig. 3). The increase in abundance in the Flathead was largely females, but sex-based population estimates were relatively imprecise especially during 2010 and 2011, the two lowest female population estimates (Fig. 3). These population estimates were generated using open mark-recapture models and were not corrected for closure bias and hence likely biased high. On average, the population estimates using spatial models were 18% lower than the open model

estimates which approximates the positive bias of the open model population estimates in this study. The open model abundance estimates were usually much more precise. Population growth averaged 1.0 (95% CI 0.96-1.06) in the Flathead during 2007-2014 while it was 0.92 (CI 0.88-0.96) in the South Rockies during 2006-2013. The growth rate in the South Rockies implies a population decline of 44% from a starting population of 272 in 2006 to 152 in 2013 (Fig. 3). The uncertainty based on the precision of the estimated growth rate implies the 2013 population size could range from 112-206 bears (95% CI). Apparent survival was similar between the units while recruitment may have been higher in the Flathead than the South Rockies (Fig. A1).

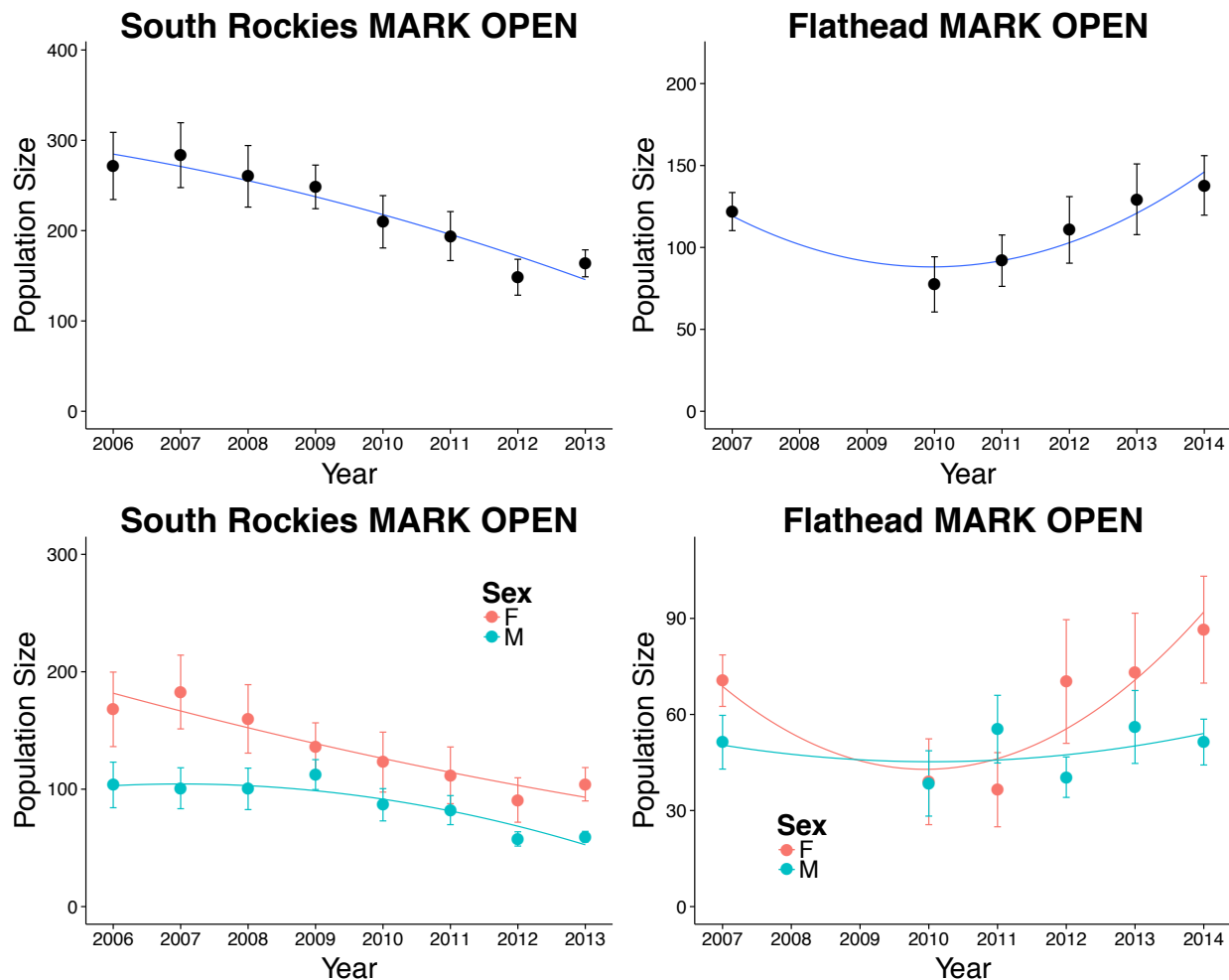


Fig. 3. Total and sex-specific population estimates for grizzly bears in the South Rockies (2006-2013) and Flathead (2007-2014) GBPU. Estimates of population size were generated from an open Pradel robust design model and error bars represent standard errors of annual population estimates.

Estimated Mortality rate

The human-caused mortality rate was similar throughout the sampling period in the Flathead while the mortality rate in the South Rockies increased as the population declined. In the South Rockies, total estimated mortality exceeded 10% during two years later in the study (Fig. 4). Female mortality rates varied among years with no clear trend in the South Rockies and a possible decline in the Flathead (Fig. 6). These female mortality rates were based on total population size (number of female kills /total population size) because that is how it is calculated in BC to inform management decisions. Managers rarely have sex-based population estimates to inform management. Hence, these data assess how managers were able to meet mortality targets using the annual estimates of population size estimated here, not the static estimate typically available to managers. In the Flathead, the total mortality rate did not exceed the target of 6% during this study (Fig. 4), despite a declining population. However, the female target of 1.8% was exceeded during 3 of 6 years (Fig. 6). In the South Rockies, the total mortality target was exceeded during 6 of 8 years (Fig. 4) and the female target was exceeded during 5 of 8 years (Fig. 6). Both targets were more often exceeded later in the study, as the population declined. Mortality targets were exceeded more often, though less drastically in some years, using the policy-based method of estimating unreported mortality (Figs. A2-A4).

Annual estimates of kill rate by sex fluctuated due to variation in population estimates stemming from sub-setting the data by sex, changes in sample size among years, as well as random influences on the small numbers of mortalities. Hence, mean mortality rates are likely more precise indicators of the limiting effect of mortality on population growth than annual estimates. The average observed mortality rate was 8.6% in the South Rockies and 4.7% in the Flathead using the data-based correction factor to account for unreported mortality (Fig. 5). Total estimated grizzly bear mortality in the South Rockies unit was higher than the 6% mortality target during this study while it was below the target in the Flathead unit (Fig. 4). The mean female kill, as a portion of total population size, was 2.9% in the South Rockies and 1.9% in the Flathead (Fig. 6). Female mortality exceeded the target by 60% in the South Rockies but only by 5% in the Flathead.

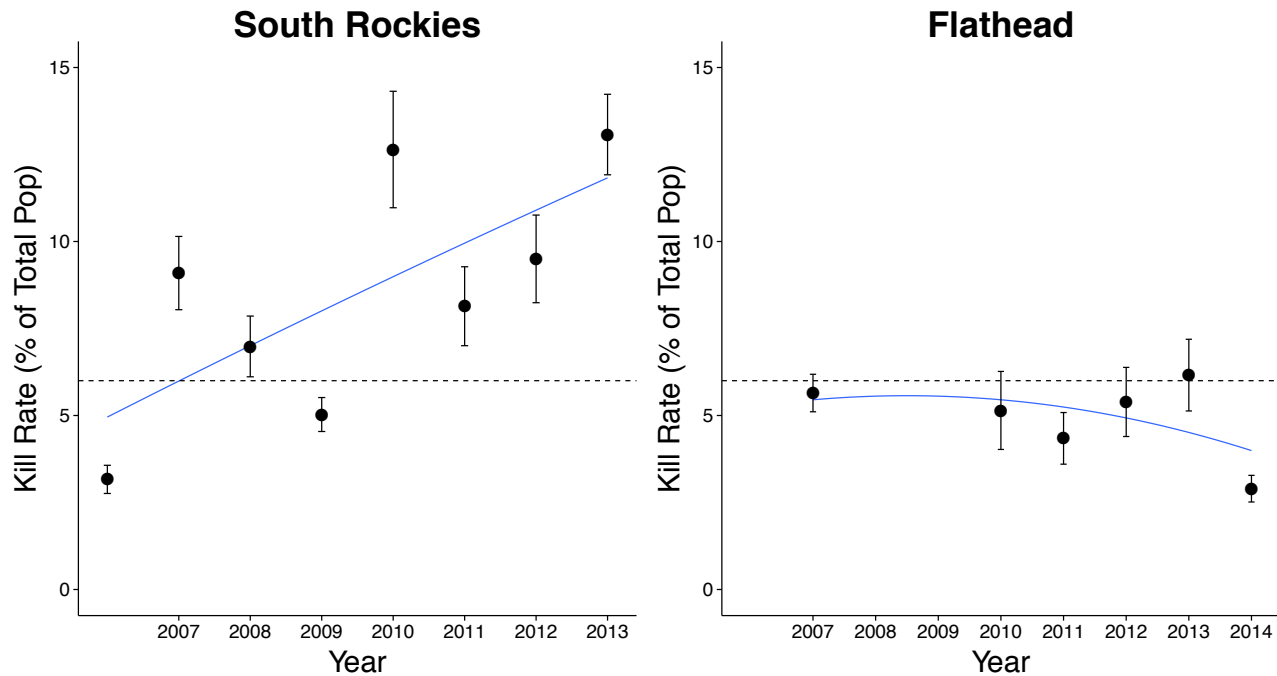


Fig. 4. Annual human-caused mortality rate of grizzly bears for the South Rockies and Flathead GBPU. The dotted horizontal line represents the 6% mortality target from the BC grizzly bear harvest procedure. Annual population estimates are from the demographic analyses above, and kill data come from the Compulsory Inspection database. Unreported mortalities were accounted for by doubling the reported non-hunter mortalities. See Fig. A2 for the policy-based method of accounting for unreported mortality. Error bars were calculated as the estimated total mortality/standard error of annual population estimate.

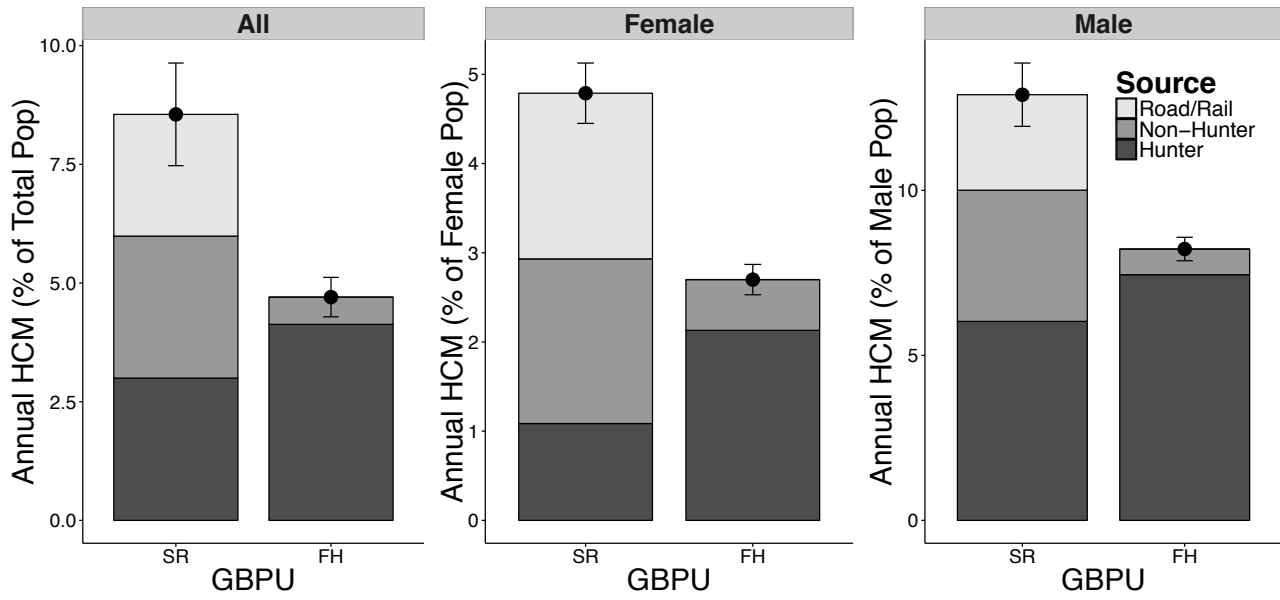


Fig. 5. Average human-caused mortality rates for the South Rockies (2006-2013) and Flathead GBPU (2007-2014) using A) estimated total mortalities and the mean population estimate during these periods, B) estimated total female mortalities and the average female population estimate and, C) estimated total male mortalities and the average male population estimate. Unreported mortalities were accounted for by doubling the reported non-hunter mortalities. Error bars were calculated as the estimated total mortality/standard error of the mean population estimate.

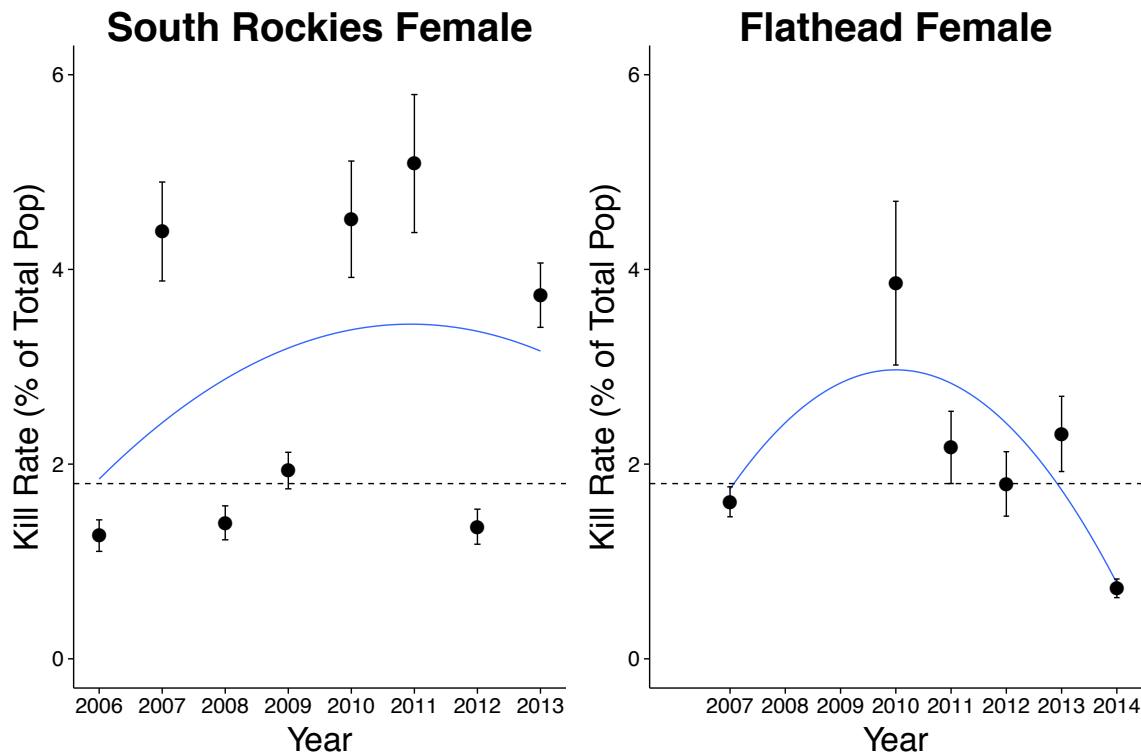


Fig. 6. Annual human-caused mortality rate of female grizzly bears for the South Rockies and Flathead GBPU. The dotted horizontal line represents the 1.8% mortality target from the BC grizzly bear harvest procedure. Annual population estimates are from the demographic analyses above, and kill data come from the Compulsory Inspection database. Unreported mortalities were accounted for by doubling the reported non-hunter mortalities. See Fig. A3 for the policy-based method of accounting for unreported mortality. Error bars were calculated as the estimated total female mortality/standard error of the annual male and female population estimate.

When available, sex-specific mortality rates should be based on population estimates for each sex because sex ratios may change due to annual differences in survival between the sexes. Using sex-specific population estimates, mortality rates of males were much higher than those of females in both populations (Figs. 5 & 7). The non-hunting male and female mortality rates increased in the South Rockies while they were lower and stable in the Flathead. The female hunting mortality rate declined during the study in both areas. The mean female mortality rate in the South Rockies was 4.7% which was one third higher than it was in the Flathead (2.7%; Fig. 5B). The mean male mortality rate was also much higher in the South Rockies (13%) than it was in the Flathead (8.5%; Fig. 5C).

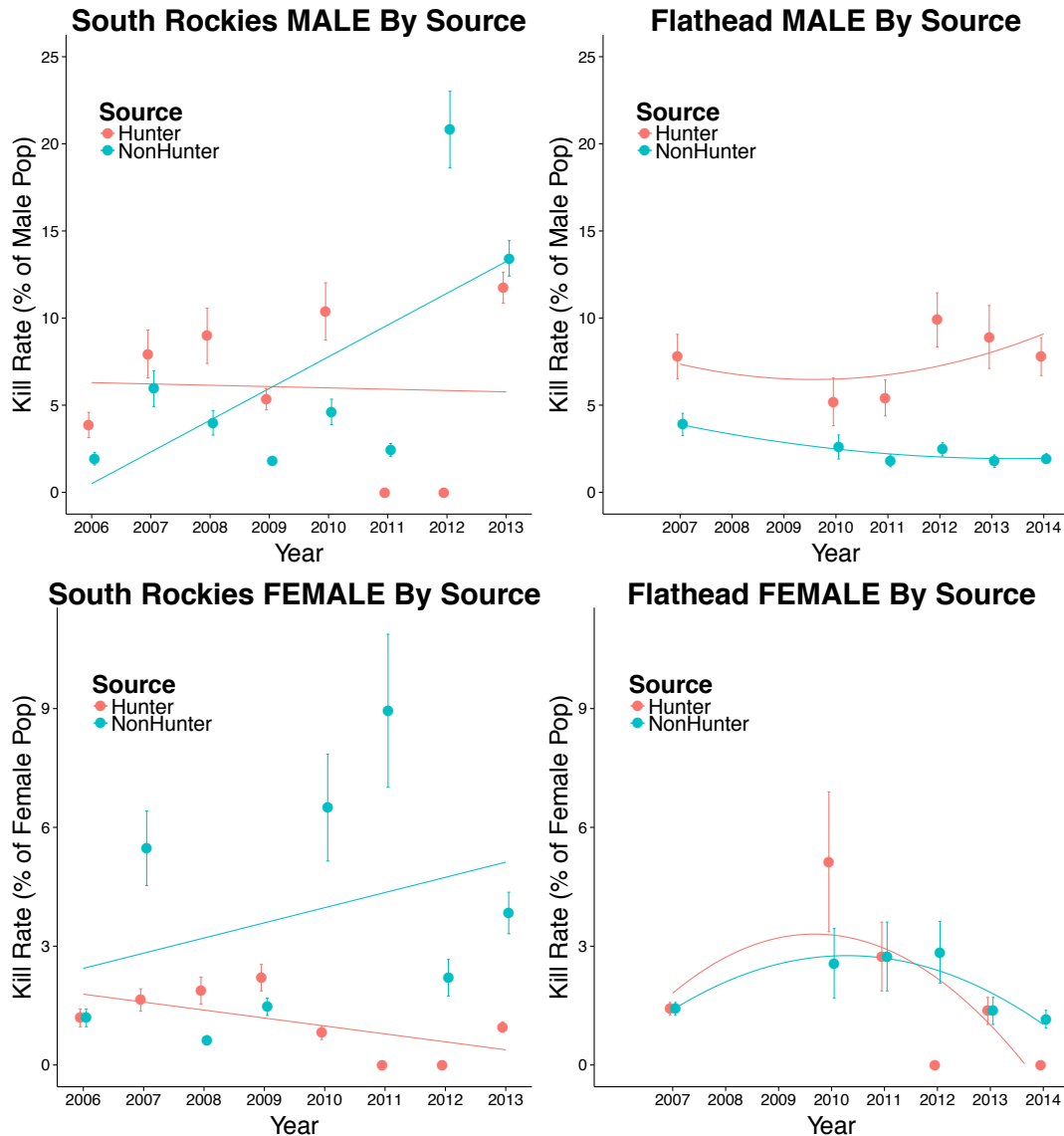


Fig. 7. Annual human-caused mortality rate of male and female grizzly bears by source (Hunter or Non-Hunter) for each GBPU as a percentage of the annual sex-specific population size. Annual population estimates are from the demographic analyses above, and kill data come from the BC Compulsory Inspection database. Unreported mortalities were accounted for by doubling the reported non-hunter mortalities. See Fig. A4 for the policy-based method of accounting for unreported mortality. Error bars were calculated as the estimated total female mortality/standard error of the annual population estimate.

DISCUSSION

The grizzly bear population in the southern Rocky Mountains of BC appears to have been declining since at least 2006. The population in the southern portion of the Canadian Flathead valley increased from at least 1979 to 1998 in spite of heavy hunting pressure, but then declined for a decade ([McLellan 2015](#)). The decline was linked to a decade of poor berry crops that caused a decrease in reproductive rates and possibly an increase in adult female mortality. The population decline in the Flathead GBPU ceased around 2010 and has since increased. This growth appears sustained given it has continued for five consecutive years. In contrast, the South Rockies population has declined by more than 40% since 2006 with no indication of recovery. A decline in berry crops may also underlie the population decline in the South Rockies, but neither annual berry production nor reproductive rates were measured in this area. During our study, observed mortality rates were higher in the South Rockies than they were in the Flathead, which may be related to the greater degree of human settlement in the South Rockies compared to the largely unsettled Flathead unit. Mark-recapture analysis, however, generated similar apparent survival estimates for the two populations which suggests bears moved into the South Rockies unit during the study. In the South Rockies, mortality rates increased as the population declined which was proximally driven by non-hunting mortality of bears. However, the ultimate cause of the increased mortality may have been the decline in forage documented in the southern Flathead valley by [McLellan \(2015\)](#).

Reproduction in the southern Flathead between 1998 and 2010 was the lowest ever recorded for grizzly bears in North America ([McLellan 2015](#)). Reproduction in the South Rockies GBPU must also have been very low because estimates of apparent recruitment there were even lower than in the Flathead GBPU. Recruitment this low has only been associated with complete berry crop failures ([McLellan 2015](#)). Immigration may partly explain the higher apparent recruitment in the Flathead than in the South Rockies because the Flathead is adjacent to a large and growing grizzly bear population to the south (Kendal et al. 2009, Mace et al. 2012) while the South Rockies is adjacent to the relatively low grizzly densities in the Central Rockies (Garshelis et al. 2005, [Mowat et al. 2013b](#)).

We believe the kill rates documented here are low because our study areas were not demographically closed because animals moved on and off the study area during our sampling. This “closure” is a key assumption of the population estimation method. Lack of closure often generates population estimates that are biased high, leading to mortality estimates that were biased low. The observed human-caused female mortality rate of 4.7% in the South Rockies was not sustainable for this population, but 2.7% was sustainable in the Flathead. In the 1980s, the human-caused mortality rate of adult females was 5.3% in the southern Flathead of Canada and yet the population was increasing at 7% per year ([McLellan 2015](#)). We used the population model

used by [McLellan \(2015\)](#) to estimate growth in the southern Flathead to estimate growth in the South Rockies GBPU. We parameterized the model with the vital rates he observed during the population decline except we used the female mortality of 4.7% observed in the South Rockies. The population growth rate predicted by this model was 0.98 which was higher than the observed growth rate (0.92 CI 0.88-0.96). We had to increase the total human-caused mortality rate of females ≥ 2 years of age to 11.7% to generate a λ of 0.92. Positive bias in the population estimates we used due to closure bias can only partly explain the discrepancy because the closure bias appears modest (18%). Thus, accounting for closure would only increase female mortality to 5.5%. We conclude that the mortality rate of females must have been much higher than the 4.7% we estimated in this study. It is probable that unrecorded adult female mortality was much higher than we estimated by simply doubling the recorded number of non-hunting human-caused mortalities. Using the policy-based method of accounting for unreported mortality generated similar results.

Our decision to double the non-hunter kills to account for unreported mortality was based on pooling data from 13 previous studies, but much of these data came from the Canadian mountain parks where few people carry firearms, and from the United States, where there is considerable human settlement but many wildlife officers ([McLellan et al. 1999](#)). Reporting of non-hunting kills may be higher in such areas than it is in remote areas with many ungulate hunters, such as our study area. It is also likely that only a portion of the rail or road mortalities are recorded and, since this component of mortality was increasing rapidly during our study, it could have generated many unreported kills. Furthermore, many railway strikes of grizzly bears involve family groups, which suggests breeding age females may be disproportionately at risk. Unfortunately, all cubs and most yearlings are known to perish if their mother is killed ([McLellan 2015](#)). If this is true, the railway or highway may have a disproportionately strong impact on population growth in the Highway 3 corridor given they only occur there (Lamb et al. In Review). When the non-hunting kill was doubled to account for unreported mortalities, highway mortality accounted for 13%, and railway mortality for 15%, of the total grizzly bear mortalities in the South Rockies GBPU during our study.

Most of the recorded non-hunting mortality in the South Rockies occurred in the Highway 3 corridor while the hunting mortality was more evenly dispersed (Lamb et al. In Review). Lamb et al. (In Review) showed that the movement of bears into the Highway 3 corridor, from both the South Rockies and Flathead units, greatly exceeded movements of bears out of the corridor, effectively extending the impact of the mortality well beyond the source. This result suggests that a relatively small area of high mortality can cause declines in grizzly numbers many kilometers from the source. Population managers must consider the landscape scale of these source/sink dynamics.

These data can only be used to evaluate the target mortality levels in the BC grizzly bear harvest procedure in a very general way. Female mortality is evaluated by provincial harvest managers based on total population size because sex-based estimates of population size are usually unavailable. The mean female mortality rate, based on the total population size, was just over the target of 1.8% in the Flathead. Though the population declined in the Flathead GBPU during our study, it also recovered with no adjustments to hunting opportunities. In earlier decades, this population increased rapidly, at about 7%/year, despite being under a similar rate of female mortality as during this study (i.e. about 3%; [McLellan 2015](#)). In the South Rockies, the mean female mortality rate, based on the total population size, was 2.9% and there was no clear sign of population recovery despite several adjustments to hunting opportunities. These results suggest female kill rates >3% of the total population size may cause prolonged population declines when the population is also food stressed, while, female kill rates <2% appear to be generally sustainable. Kill rates between 2 and 3% probably also risk causing population decline during periods of limited food supply. In this arguably worst case, the target female kill of 1.8% appears to present a moderate level of conservation risk. True kill rates were probably higher during the study because our population estimates were likely positively biased which would have biased our estimated kill rates low. In addition, unreported kills were likely much higher than we estimated which would also have contributed to underestimating kill rates. In populations that are not food stressed the current BC mortality target likely presents low conservation risk. The total kill rate in the South Rockies also exceeded the target level of 6% however, large mammal population growth rates are typically only influenced by male mortality rates when mortality levels reach the point there are so few males remaining that pregnancy rates are reduced. This has rarely been documented in any species of large mammal. It is very unlikely to happen with grizzly bears because females only breed every 3-4 years so, compared to species that breed annually, fewer males are required to breed all the females in estrous. The total mortality target protects the population more by limiting the female kill than by limiting the total kill. Even if there was no female target, females rarely exceed 36% of the kill in these two GBPU's hence, the female kill will normally be below 2.2% of the total population size when the mortality target for both sexes is 6%.

The larger management question is how the harvest procedure works when a population is in decline. In this study, there was circumstantial evidence that the population decline was caused by an interaction between food supply limiting reproduction and high human-caused mortality. However, the cause of decline in free ranging wildlife populations is often unknown. Probably many population declines and recoveries happen without being detected by population managers because tools and funds for monitoring are limited. Mortality management for grizzly bears in BC is based on a population prediction or estimate, hence inventory, not on monitoring population trends. And, while more focus could be put on monitoring trends, it may be required only in those few populations where estimated mortality rates are highest and cannot be reduced by limiting hunting opportunities because non-hunting mortality is high. Population monitoring will never be

possible in the majority of the province, so the harvest procedure must be robust to undetected changes in population size. Practically this means setting conservative mortality rates or, incorporating trends in abundance or auxiliary indices of food in the harvest procedure.

Exceeding a mortality target does not necessarily imply a population decline. When a target is exceeded managers respond by reducing hunting opportunity and examining the recent trend in non-hunting mortality. Efforts to reduce non-hunting mortality may follow. Although population growth depends on vital rates which can change, in most cases the mortality target is not a threshold level above which population decline is inevitable. The current target rate of 6% was sufficient to protect the Flathead population even during a decade long berry failure because target kill levels were not exceeded. However, this population appears to have little non-hunting mortality, while the opposite is true for the South Rockies where the population decline was substantial and non-hunting mortality was high and likely underestimated.

The problem in the South Rockies unit appears to have been the increase in mortality rate during the population decline. This may be a common occurrence in grizzly bear populations near settled areas because food shortages often lead to more human-bear conflicts and higher bear mortality ([Pease and Mattson 1999](#), [Gunther et al. 2012](#)). Human-caused mortality of adult bears was very high in Owikeno Inlet on the central coast of BC following the collapse of the sockeye run into the inlet ([Boulanger et al. 2004](#)). In our study area, many bears acquire most of the fat needed for hibernation and reproduction eating huckleberries ([McLellan 2011](#)), which grow well away from where humans live and travel. A huckleberry failure may force bears to search for food closer to humans which can lead to higher mortality during periods of low food ([McLellan 2015](#)). Population managers should monitor the trend in non-hunter mortality so they can promptly respond to increases and maintain total kill below targets. The trend in non-hunting mortality may also be useful as a simple method to detect possible declines in grizzly food or abundance. This index must be used in conjunction with other information ([Mowat et al. 2013b](#)) because increased human conflict may also happen when the population is increasing.

[Regehr et al. \(2015\)](#) suggested female survival, juvenile recruitment and carrying capacity are useful metrics that could collectively monitor polar bear persistence. Many population monitoring programs measure survival and recruitment, including the study presented here, but few studies are able to index or measure carrying capacity through time. [Regehr et al.](#) suggested monitoring the growth rate itself as an index of carrying capacity. Growth at or near the maximum observed rate for the species suggests the population is well below carrying capacity. No growth suggests the population is near carrying capacity and, negative growth suggest the population is above carrying capacity. However the trend must be stable over several years to calculate the growth rate with adequate precision and to ensure it is not being affected by latent age effects. More importantly perhaps, human-caused mortality must be trivial or completely recorded. Using the

observed growth rate to detect changes in carrying capacity will likely only work in very well-studied species like polar bears, but even then it is only likely to happen in a few populations. Perhaps a better option for grizzly bears in BC would be to derive simple indices to annually monitor the most important foods for bears such as salmon, huckleberries, buffaloberries, whitebark pine cone production, ungulates and herbaceous vegetation. For the vegetative foods, indices derived from weather data would be ideal because this data is currently collected. These indices could then be used to identify recent declines in major food which may signal the need to reduce grizzly bear mortality targets.

The number of grizzly bear hunting tags awarded to resident hunters is based on recent hunter success such that more tags are issued when success declines. A prolonged reduction in success may be due to a population decline and, responding to a decline by increasing hunter effort could exacerbate the decline. Setting static resident tag numbers based on past success (during a period of population stability) and not increasing tag numbers due to lower recent success would reduce, but not eliminate, the risk that resident hunting becomes depensatory.

For decades, the Elk valley in the South Rockies population unit has had the highest number of grizzly bear conflict calls to the Conservation Officer Service in the Kootenay Region. Non-hunter mortalities in the Elk valley have also far exceeded mortalities in other parts of the Kootenays and, most areas of the province. The increasing non-hunter mortality is of particular concern in this area. Hunting harvest is relatively easy to adjust, while there are many challenges in mitigating non-hunting mortality. Fernie and the Elk valley have had a WildSafeBC program (formerly Bear Aware) since 2005. Elk valley residents and businesses are knowledgeable about bear conflicts and have taken advantage of the educational programs available in the valley. Despite this public engagement and awareness, conflict kills continue to rise suggesting that reducing the kill level will take concerted planning, and energy to implement these new plans. The rapid increase in road and rail mortalities is of particular concern because it is not easily addressed.

The population decline documented by McLellan (2015) in the southern Flathead may be broad scale. Analysis of hunter killed male grizzly bears using age-at-death methods (Skalski et al. 2005) estimated the grizzly population trend in the entire Kootenay Region increased from 1980 to 2004 and then declined until about 2013 with a small recovery thereafter (Ian Hatter, In preparation). The weather events that caused berry crop failures in the Flathead valley may have had similar effects across southeast BC, triggering a broad grizzly bear population decline. A concurrent decline in berry production was measured in the Cabinet mountains 130 km southwest of the Flathead valley ([Holden et al. 2012](#)). While human-caused mortality is likely one factor explaining the ongoing decline in the South Rockies, it is insufficient to explain the decline across the entire region because almost all parts of the region have much lower mortality rates than recorded in either of the populations studied here. Food limitation was probably the ultimate cause of the

decline while recruitment and mortality were proximate causes. Increases in human-caused mortality following a food shortage do not appear to occur throughout the grizzly bear range in BC but rather seem to be centered around areas where humans live in good bear habitat.

This work demonstrates the importance of population monitoring to determine the trend of populations of concern. A single open model analysis of the entire dataset clearly demonstrated the trend in both populations. This study also demonstrates that population monitoring using hair sampling and modest annual effort can generate precise estimates of population parameters with as few as six years of sampling. This sort of monitoring may also be useful in other places in BC where mortality is high or populations are small and at risk. Monitoring survival and reproduction of a sample of collared bears can provide similar data on population trend as well as a variety of other important information. In particular, collared bears can provide insights into causes and rates of unrecorded mortalities which appear to be major factors influencing these populations.

Sample coverage was not complete in all years which can lead to unequal capture probabilities for individuals among years and can bias both survival and recruitment estimates, and hence the population growth rate. The risk of bias was greatest for females because some have small home ranges, and individual movement may have been insufficient to ensure recapture probabilities were similar among bears. We amended the study area boundary to include only areas that were sampled every year to ensure these changes in sample coverage did not bias the estimates of demographic parameters. The growth rate for the South Rockies was 0.90 using the full study area and was 0.92 in the reduced study area suggesting this bias was modest. We also adjusted the boundary in the Flathead, but there was no change in the growth rate because few bears were ever captured in the excluded area (the Galton Range).

Variation in capture probabilities among individuals may be caused by factors other than gender, such as body size or partial residency in the study area. Cubs are particularly small early in the year and, though other authors have confirmed detection of cubs at bait sites ([Kendall et al. 2009](#)), it is likely that cubs have lower detection probabilities early in the year and, that detections increase as cubs get larger and are not as tightly controlled by their mothers. Not all individuals, particularly females, appear to rub on trees in a given year ([Clapham et al. 2012](#), [Lamb et al. In press](#), [McLellan and McLellan, In Prep](#)) which would cause considerable heterogeneity in detection success within years. Similarly, partial residency by individuals that live on the edge of the study area is a known cause of capture heterogeneity ([Efford 2004](#)). Heterogeneity in detection success is likely always present, but open models are generally robust to this issue ([Williams et al. 2001](#)). In our study, the estimated parameters such as apparent survival, apparent reproduction, and population growth were likely robust to heterogeneity, but population estimates were more likely to be biased. Closed spatial capture-recapture models are preferable for estimating population size because they accommodate most forms of capture heterogeneity and are not biased by the spatial

arrangement of traps ([Efford 2004](#)). Closed model population estimates of abundance would have been preferable for estimating kill rates, but we did not have enough data to run closed models during many years of this study. In conclusion, we believe our mark-recapture based estimates of survival, reproduction, and population growth are accurate and our estimates of population size were generally biased high but were likely biased low during years when there was little or no bait site sampling. The positive bias in population estimates was likely modest (about 18%).

MANAGEMENT RECOMMENDATIONS

1. Investigate ways to reduce non-hunting grizzly bear kills and increase public safety in the backcountry. This will require consultation with backcountry users to be successful. Some options include: mandatory use of bear spray even for hunters; programs to protect camps and especially meat in the backcountry such as loaner electric fences; and road or trail closures in areas where conflict is high.
2. Quantify road and rail mortality of grizzly bears in the parts of the province where road/rail kills are significant, such as parts of the Highways 1, 3 and 16 corridors.
3. Investigate past rates of unreported mortality by doing a meta-analysis of all past and present grizzly bear survival studies in BC. The goal is to quantify what proportion of radio-collared bears that are killed by people is being recorded in the compulsory reporting system.
4. Unreported mortality should be accounted for in the harvest procedure as a portion of the reported non-hunter mortality. This will make the harvest system responsive to changes in mortality factors.
5. Implement simple ways to monitor major grizzly bear food resources annually. Food types such as salmon, huckleberries, buffaloberries, and green vegetation could be useful starting points.
6. Implement population trend monitoring in areas of the province with chronically high grizzly bear mortality.
7. Set grizzly bear resident hunter tag numbers at the beginning of each allocation period based on past success and, do not increase tag numbers during the 5-year allocation cycle if success goes down.
8. If measures to reduce non-hunting mortality are not successful, reduce the target mortality rate in the grizzly bear harvest procedure to ensure the hunt is sustainable during periods of food shortage.

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LITERATURE CITED

- Anderson, D. R., and K. P. Burnham. 2002. [Avoiding Pitfalls When Using Information-Theoretic Methods. The Journal of Wildlife Management 66:912–918.](#)
- Artelle, K. A., S. C. Anderson, A. B. Cooper, P. C. Paquet, J. D. Reynolds, and C. T. Darimont. 2013. [Confronting uncertainty in wildlife management: Performance of grizzly bear management.](#)
- Boulanger, J., S. Himmer, and C. Swan. 2004. [Monitoring of grizzly bear population trends and demography using DNA mark–recapture methods in the Owikeno Lake area of British Columbia. Canadian Journal of Zoology 82:1267–1277. DOI 10.1139/z04-100](#)
- Boulanger, J., K. C. Kendall, J. B. Stetz, D. A. Roon, L. P. Waits, and D. Paetkau. 2008. [Multiple data sources improve DNA-based mark-recapture population estimates of grizzly bears. Ecological Applications 18:577–589.](#)
- Clapham, M., O. T. Nevin, A. D. Ramsey, and F. Rosell. 2012. [A Hypothetico-Deductive Approach to Assessing the Social Function of Chemical Signalling in a Non-Territorial Solitary Carnivore. PloS one 7:e35404.](#)
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- Elfström, M., A. Zedrosser, O. G. Støen, and J. E. Swenson. 2014. [Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: Review and management implications. Mammal Review 44:5–18.](#)
- Gardner, B., J. Reppucci, M. Lucherini, and J. A. Royle. 2010. [Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. Ecology 91:3376–3383.](#)

- Garshelis, D. L., M. L. Gibeau, and S. M. Herrero. 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. *Journal of Wildlife Management* 69:277–297.
- Grizzly Bear Study Team. 2008. Grizzly Bear Population and Density Estimates for Alberta Bear Management Unit 6 and British Columbia Management Units 4-1, 4-2, and 4-23 (2007). Alberta Sustainable Resource Development.
- [Gunther, K. A., M. A. Haroldson, K. Frey, S. L. Cain, J. Copeland, and C. C. Schwartz. 2004. Grizzly bear–human conflicts in the Greater Yellowstone ecosystem, 1992–2000. *Ursus* 15:10–24.](#)
- [Haroldson, M., M. Ternent, K. Gunther, and C. Schwartz. 2002. Grizzly bear denning chronology and movements in the Greater Yellowstone Ecosystem. *Ursus* 13:29–37.](#)
- [Holden, Z. A., W. F. Kasworm, C. Servheen, B. Hahn, and S. Dobrowski. 2012. Sensitivity of berry productivity to climatic variation in the Cabinet–Yaak grizzly bear recovery zone, Northwest United States, 1989–2010. *Wildlife Society Bulletin* 36:226–231.](#)
- [Huggins, R. M. 1991. Some Practical Aspects of a Conditional Likelihood Approach to Capture Experiments. *Biometrics* 47:725–732.](#)
- [Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. *Journal of Wildlife Management* 73:3–17.](#)
- [Laake, J. 2013. RMark : An R Interface for Analysis of Capture-Recapture Data with MARK.](#)
- [Lamb, C. T., G. Mowat and D. A. Walsh. Factors influencing detection success of grizzly bears at genetic sampling sites. *Ursus*: In Press.](#)
- Lamb, C., G. Mowat, B. N. McLellan, S. Boutin. In Review. Human settlement creates an ecological trap for grizzly bears in a region rich in fruit resources. Submitted to *Journal of Applied Ecology*.
- [Lebreton, J., and K. Burnham. 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals : A Unified Approach with Case Studies. *Ecological Monographs* 62:67–118.](#)
- Mace, R. D., D. W. Carney, T. Chilton-Radandt, S. A. Courville, M. A. Haroldson, R. B. Harris, J. Jonkel, B. N. McLellan, M. Madel, and T. L. Manley. 2012. Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. *The Journal of Wildlife Management* 76:119–128.
- [McLellan, B. N., F. W. Hovey, R. D. Mace, J. G. Woods, D. W. Carney, M. L. Gibeau, W. L. Wakkinen, and W. F. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management* 63:911–920.](#)
- [McLellan, B. N., and F. W. Hovey. 2001. Natal dispersal of grizzly bears. *Canadian Journal of Zoology* 79:838–844.](#)

- McLellan, B. N. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. *Canadian Journal of Zoology* 89:546–558.
- McLellan, B. N. 2015. Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *The Journal of Wildlife Management* 79: 749–765.
- Mowat, G., D. C. Heard, D. R. Seip, K. G. Poole, G. Stenhouse and D. W. Paetkau. 2005. Grizzly and black bear densities in the interior mountains of North America. *Wildlife Biology* 11:41-58.
- Mowat, G., M. Efford, B. McLellan, and S. Nielsen. 2013a. South Rockies & Flathead Grizzly Bear Monitoring Final Report 2006-2011. BC Ministry of Forests, Lands, and Natural Resource Operations. Available from http://www.researchgate.net/profile/Garth_Mowat/publication/255970768_South_Rockies_Flathead_Grizzly_Bear_Monitoring/links/00b49521522e83883c000000.pdf (accessed December 18, 2015).
- Mowat, G., D. C. Heard and C. J. Schwarz. 2013b. Predicting grizzly bear density in western North America. *PLoS One*. 8(12): e82757.
- Nichols, J., and J. Hines. 2002. Approaches for the direct estimation of u , and demographic contributions to u , using capture-recapture data. *Journal of Applied Statistics* 29:539–568.
- Pease, C. M. and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bear. *Ecology* 80:957-975. DOI: 10.1890/0012-9658(1999)080[0957:DOTYGB]2.0.CO;2
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Proctor, M., and B. McLellan. 2004. Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Canadian Journal of Zoology* 1118:1108–1118.
- Proctor, M. F., D. Paetkau, B. N. McLellan, G. B. Stenhouse, K. C. Kendall, R. D. Mace, W. F. Kasworm, C. Servheen, C. L. Lausen, and M. L. Gibeau. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs* 180:1–46.
- Proctor, M. F., S. E. Nielsen, W. F. Kasworm, C. Servheen, T. G. Radandt, A. G. Machutchon, and M. S. Boyce. 2015. Grizzly bear connectivity mapping in the Canada–United States trans-border region. *The Journal of Wildlife Management* 79:544–558.
- Regehr, E. V., R. R. Wilson, K. D. Rode, and M. C. Runge. 2015. Resilience and risk: a demographic model to inform conservation planning for polar bears. US Geological Survey. Available from <http://pubs.er.usgs.gov/publication/ofr20151029> (accessed December 18, 2015).
- Skalski, J. R., K. E. Ryding, and J. Millspaugh. 2010. *Wildlife Demography: Analysis of Sex, Age, and Count Data*. Academic Press.
- Stoen, O.-G., A. Zedrosser, S. Saebo, and J. E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* 148:356–364.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations First Edition. Academic Press, San Diego, USA.

APPENDIX

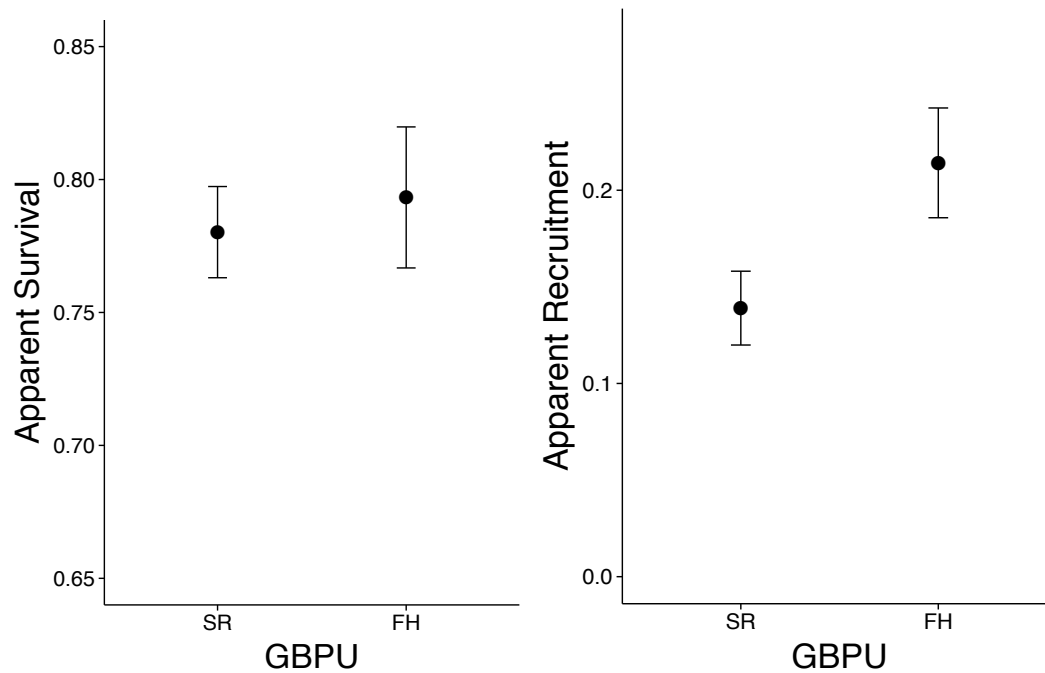


Fig. A1. Mean apparent survival and recruitment rates for the South Rockies GBPU during 2006-2013 and the Flathead GBPU during 2007-2014.

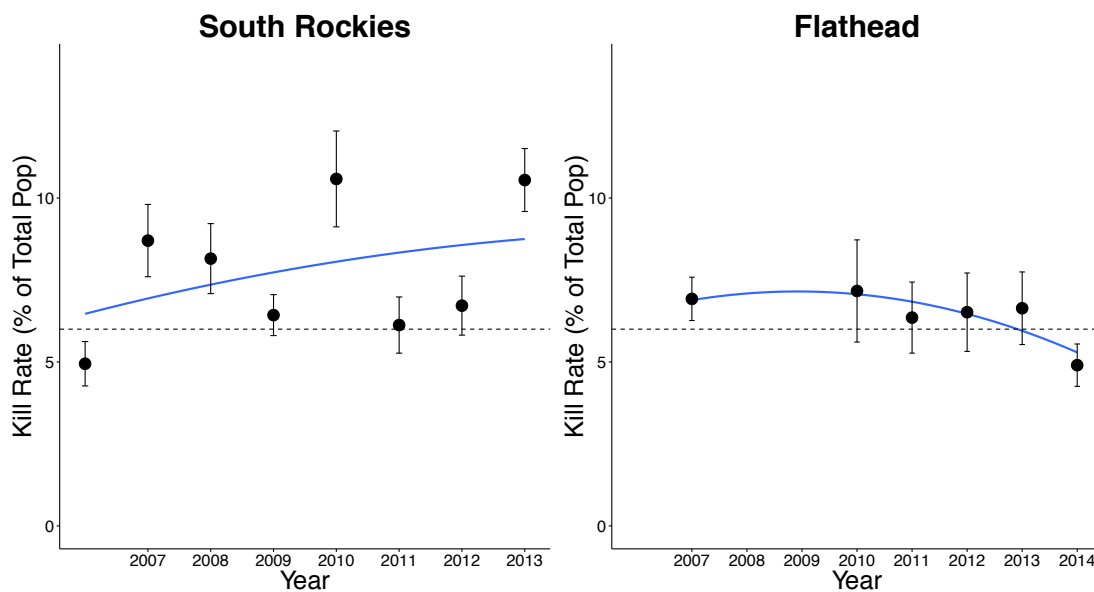


Fig. A2. Annual human-caused mortality rate of grizzly bears for each GBPU. The dotted horizontal line represents the 6% harvest policy cap. Annual population estimates are from the demographic analyses above, and kill data come from the Compulsory Inspection database. Unreported mortalities were accounted for by adding 2% to the observed mortality rate.

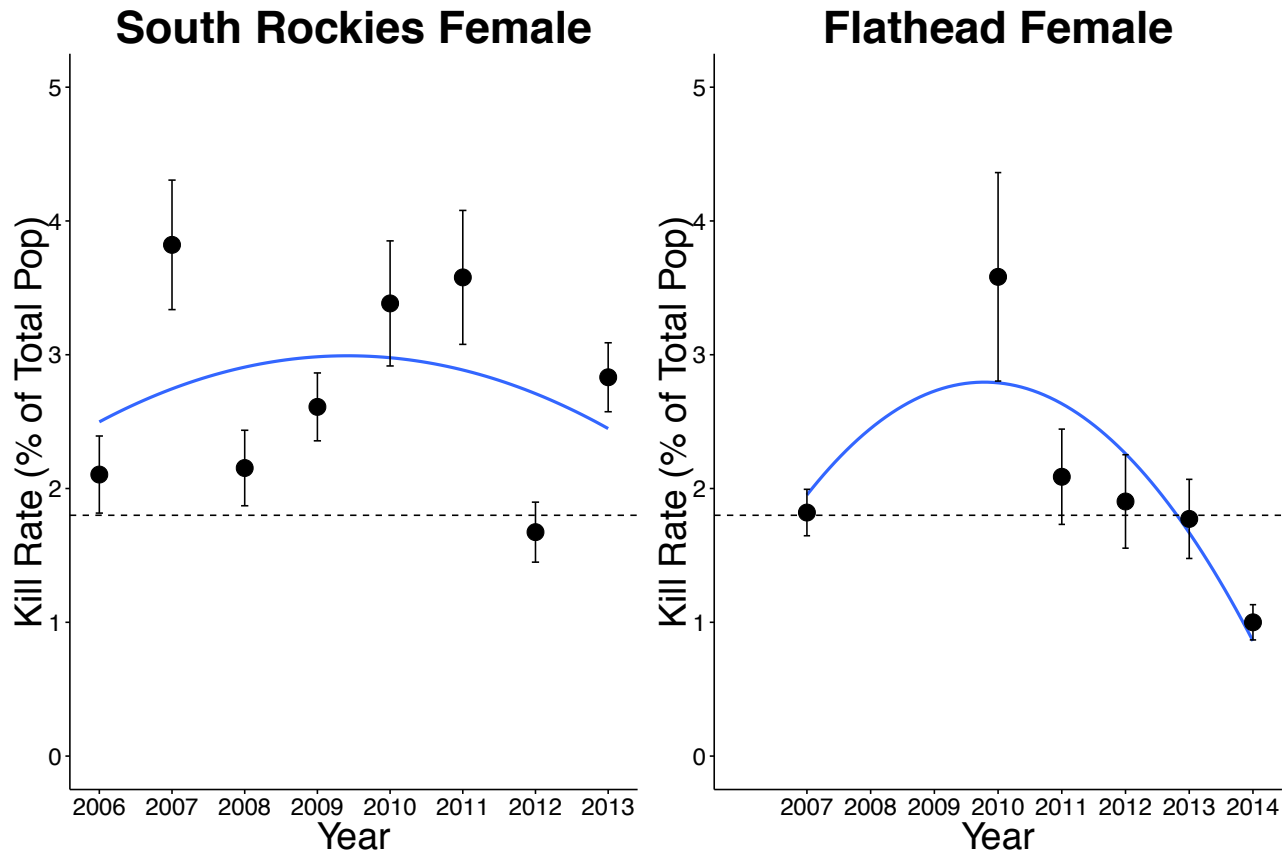


Fig. A3. Annual human-caused mortality rate of female grizzly bears for each GBPU. The dotted horizontal line represents the 1.8% target mortality level. Annual population estimates are from the demographic analyses above, and kill data come from the Compulsory Inspection database. Unreported mortalities were accounted for by adding 1% to the observed mortality rate.

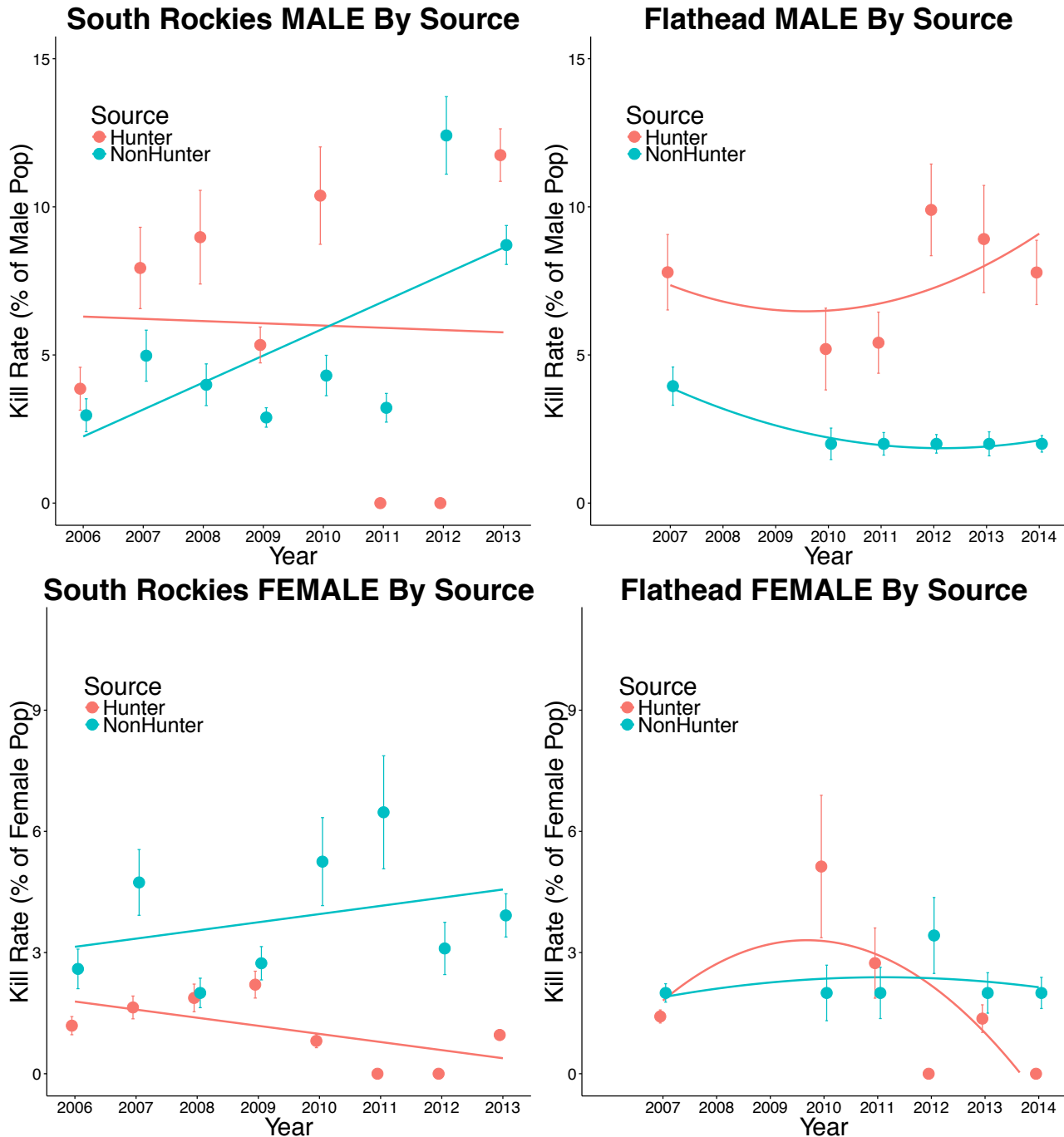


Fig. A4. Total annual human-caused mortality rate of male and female grizzly bears by source (Hunter or Non-Hunter) for each GBPU as a percentage of the sex-specific population size. Annual population estimates are from this study, and kill data come from the Compulsory Inspection database. Unreported mortalities were accounted for by adding 2% to the observed mortality rate.

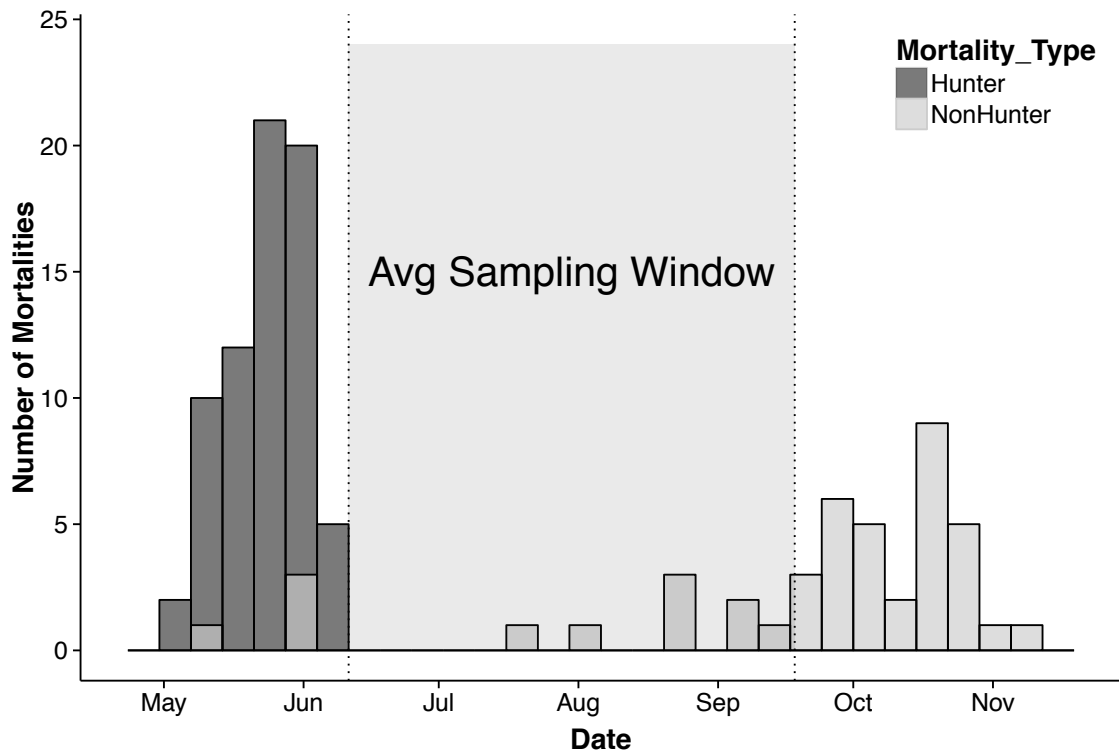


Fig. A5. The relationship between the timing of non-invasive genetic sampling and the timing of human-caused bear mortalities in the South Rockies and Flathead grizzly bear population units during 2006-2013. Many mortalities within the average sampling window would suggest a violation of the closure assumption during sampling of the secondary sessions. However, our sampling did not begin until after the hunting season and the majority of non-hunting kills happen in fall, after our sampling was completed.



Research

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Demographic mechanisms underpinning genetic assimilation of remnant groups of a large carnivore

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Current range expansions of large terrestrial carnivores are occurring following human-induced range contraction. Contractions are often incomplete, leaving small remnant groups in refugia throughout the former range. Little is known about the underlying ecological and evolutionary processes that influence how remnant groups are affected during range expansion. We used data from a spatially explicit, long-term genetic sampling effort of grizzly bears (*Ursus arctos*) in the Northern Continental Divide Ecosystem (NCDE), USA, to identify the demographic processes underlying spatial and temporal patterns of genetic diversity. We conducted parentage analysis to evaluate how reproductive success and dispersal contribute to spatio-temporal patterns of genetic diversity in remnant groups of grizzly bears existing in the southwestern (SW), southeastern (SE) and east-central (EC) regions of the NCDE. A few reproductively dominant individuals and local inbreeding caused low genetic diversity in peripheral regions that may have persisted for multiple generations before eroding rapidly (approx. one generation) during population expansion. Our results highlight that individual-level genetic and reproductive dynamics play critical roles during genetic assimilation, and show that spatial patterns of genetic diversity on the leading edge of an expansion may result from historical demographic patterns that are highly ephemeral.

1. Introduction

Worldwide, many large terrestrial carnivores suffered population declines and extirpation from much of their range during the nineteenth and early twentieth centuries [1–4]. Though some populations continue to decline or remain imperilled, many populations are now stable or rapidly recovering [5]. Given the crisis nature of conservation biology [6], most research focuses on determining the mechanisms underpinning population decline, range contraction, or extirpation. On the other hand, understanding of the recovery process and subsequent range expansion following contraction is based largely on theoretical simulations [7–13] and historical reconstructions [14–17], and thus relies heavily on idealized scenarios. This is particularly true for large carnivores, as detailed data collected at appropriate spatial and temporal scales necessary for tracking expansion processes in long-lived and highly mobile organisms are extraordinarily rare.

Population genetic theory generally predicts greater differentiation and lower genetic diversity on the leading edge of range expansions [7–11,13]. This pattern arises from the long-distance dispersal of small numbers of founding individuals at the edges of the expansion zone. Typically, gene flow (dispersal) between populations increases as the contiguous population continues to expand, leading to greater similarity between populations at the range core and on the periphery [7,12,18]. However, when remnant groups

exist in the direct path of the core expansion, the manner and timescale of assimilation is currently unknown, and probably depends on reproductive success, dispersal rate, and habitat carrying capacity [7,10,12]. Initially, remnant groups tend to have low genetic diversity due to generations of relative isolation, low effective population sizes, and subsequent genetic drift. Theoretical simulations suggest that during population expansion an infusion of dispersers from the neighbouring core and subsequent interbreeding between populations function to increase genetic diversity within peripheral populations [7,8,13].

Numerous populations of carnivores persist as remnants [19–29], largely due to habitat fragmentation and persecution, with climate change expected to exacerbate the problem in additional populations [30]. Nevertheless, few studies have examined fine-scale interactions between expanding core populations and existing remnant groups because the temporal and spatial data necessary to do so are rarely available. Empirical studies at the ecosystem scale at which large carnivores function can reveal patterns in spatial genetic diversity and help identify the underlying ecological and evolutionary processes responsible for observed patterns. Demographic dynamics (e.g. dispersal, reproduction, and carrying capacity), in particular, probably have a very strong impact on contemporary evolutionary processes responsible for spatio-temporal patterns of genetic diversity observed during ongoing range expansions.

Logistically, investigating reproductive success and dispersal in large carnivores is exceedingly difficult given the challenges posed by the life history and ecology of most species. Many large carnivores are solitary and most are wide-ranging, making observational assessments of maternity difficult and paternity nearly impossible to ascertain. Migration and dispersal studies traditionally use mark–recapture or tracking technologies to follow individuals over time, but often suffer from insufficient sample sizes and focus on subsets of ecosystems due to the monetary expenses and time involved. Inferred methods (e.g. parentage/kinship analysis) have therefore been the preferred method of reconstructing kin relationships [31–41]. However, large carnivores are often long-lived and have overlapping generations, making it difficult to obtain the spatial and temporal genetic data needed to construct accurate pedigrees. Given these challenges, no study has evaluated how demographic phenomena occurring in remnant, low-density groups and an expanding core influence subsequent patterns of intraspecific genetic diversity in large carnivores.

Grizzly bears (*Ursus arctos*) in the contiguous USA survive in four geographically separated populations [42], a fraction of their former range. Only two of these, the Northern Continental Divide Ecosystem (NCDE) and the Greater Yellowstone Ecosystem (GYE) support more than approximately 80 individuals. Dispersal between populations is rare, especially for females [43], but does occur in limited cases [44], and the NCDE population remains connected to Canadian populations. The NCDE population was listed as threatened in 1975 [45], but has been showing signs of recovery, both in terms of occupied range [46] (Mace R, Roberts L. 2012 Northern Continental Divide Ecosystem Grizzly Bear Monitoring Team Annual Report, 2012. Montana Fish, Wildlife & Parks, 490 N. Meridian Road, Kalispell, MT 59901, 2012, unpublished data) and population abundance, growing from approximately 765 individuals in 2004 [46] to

nearly 1 000 individuals in 2009 [47]. Historically, Glacier National Park (GNP), in the most northern NCDE, was a stronghold for the population with higher protection afforded to individuals within park boundaries resulting in fewer human-caused mortalities [45]. Partly as a result, GNP and adjacent lands, henceforth referred to as the core, had high densities of grizzly bears, while lands further south supported low densities of bears that were probably semi-isolated when populations were smaller, as evidenced by historical genetic structure [46].

The combination of an incomplete range contraction and subsequent expansion provides a valuable natural experiment using grizzly bears as a model carnivore species. Grizzly bears can reach nearly 30 years of age [47], have overlapping generations with a generation length of approximately 10 years [48], and exhibit many of the same traits that make studying other large carnivores difficult. Here, we use extremely rare, highly rigorous spatial and temporal grizzly bear genetic data collected at an ecosystem scale to (i) evaluate the spatial and temporal dynamics of genetic diversity during grizzly bear population growth and range expansion in the NCDE and (ii) identify the underlying demographic processes responsible for spatial and temporal fluctuations in genetic diversity.

2. Material and methods

(a) Study area

The 32 000 km² NCDE is one of the largest and most intact ecosystems in the USA. The vast majority of land is protected mountainous terrain, encompassing GNP, all or portions of five national forests (Flathead, Lolo, Lewis & Clark, Lincoln, and Kootenai), five wilderness areas (Bob Marshall, Scapegoat, Great Bear, Mission Mountain, and Rattlesnake), three wilderness study areas (Mount Hefty Tuchuck, Thompson-Seton, and Ten Lakes), parts of the Blackfoot Nation and Confederated Salish and Kootenai Reservations, along with private land holdings located mostly on the eastern, western, and southern periphery. Waterton Lakes National Park in Alberta, Canada, is adjacent to the northern boundary of the NCDE.

(b) Genetic samples

Two independent sampling methods were used to collect genetic samples (bear hair) from 1998–2012: (i) hair traps—corrals of barbed wire with lure in the centre systematically distributed using an 8 × 8 km (1998, 2000) or 7 × 7 km (2004) grid and (ii) bear rubs—naturally occurring trees or other objects that bears rub on fitted with barbed wire (1998–2000, 2004, and 2009–2012). From 1998 to 2000, sampling occurred on 8 000 km² in the northern extent of the NCDE (north of Highway 2 (figure 1)), whereas systematic and consistent, ecosystem-wide sampling occurred in 2004 and 2009–2012. In total, there were 6 160 confirmed grizzly bear detections, leading to the identification of 1 115 unique individual genotypes (520 male, 595 female). All samples were originally genotyped at seven variable microsatellite loci to identify unique individuals (G10J, G1A, G10B, G1D, G10H, G10M, and G10P). We then attempted to extend genotypes of a subset of samples to 16 ($n = 142$) (previous seven loci in addition to G10C, CXX110, CXX20, G10L, MU50, MU59, G10U, MU23, and G10X) and 24 markers ($n = 637$) (previous 16 loci in addition to REN145.P07, MSUT2, CPH9, MU51, REN144.A06, MU26, D123, and D1A) as resources and sample material allowed (electronic supplementary material, tables S1 and S2). Individuals were also genotyped at amelogenin to identify gender [49]. We sampled 71% (95%

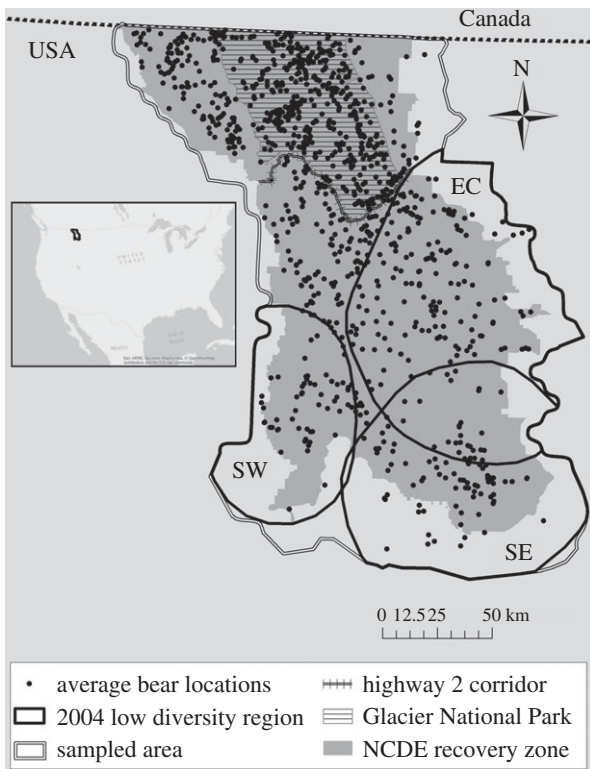


Figure 1. Average locations of 1115 individual grizzly bears in the Northern Continental Divide Ecosystem (NCDE), USA, between 1998 and 2012. Black polygons encompass buffered regions of interest due to low heterozygosity (H_0) in 2004, clipped by the sampled study area (double lines).

CI = 66–76%) of the population in 2004 [46] suggesting that most individuals first identified in 2009–2012 are younger bears. Further details on data collection, laboratory protocol, molecular analysis, and data quality control are available in Kendall *et al.* [46]. Samples collected from 2009 to 2012 were processed in the same laboratory with the same procedures as Kendall *et al.* [46]. Assuming a 2–3% annual rate of increase in the NCDE population [47], approximately 30–35% of the population was sampled annually from 2009 to 2012.

(c) Spatial genetic diversity

To describe spatial patterns of genetic diversity (Objective 1), we split samples into three time periods: samples collected in 2004 (545 individuals), 2009–2010 (449 individuals), and 2011–2012 (494 individuals). Within each time period, we averaged locations of individuals that were detected more than once. We performed calculations with the seven loci that were genotyped consistently (electronic supplementary material, table S2) across study years and individuals. We found positive spatial autocorrelation of genotypes out to 66 km using *Genalex* 6.5 [50] (electronic supplementary material, figure S1), and subsequently used this to define the extent of the neighbourhood used for calculating spatial patterns in genetic diversity. We calculated six metrics of local genetic diversity using a radius of 33 km in a moving-window analysis with the spatial Genetic Diversity package (sGD) [51] for the R statistical environment [52]. We calculated metrics when more than or equal to 10 individuals were contained within the 33 km radius of each focal individual.

(d) Parentage analysis

We used the full-pedigree likelihood approach implemented in COLONY 2.0 [52–54] to identify familial relationships among grizzly bears in the NCDE. COLONY iteratively substitutes individuals into clusters of family groups based on genotypes to

determine the most parsimonious family tree configuration [53–55] and has been shown to be quite accurate (80–100% correct assignments) with more than or equal to 10 loci genotyped when run on a simulated population with similar attributes to the NCDE grizzly bear population [56]. This method also infers genotypes of non-sampled parents. All 1115 genotypes were included in the analysis. Missing alleles are dropped from analysis so that individuals genotyped at fewer loci are compared only at available loci. We report parentage results from a single long run in COLONY (approx. 300 million iterations) using all data where we allowed polygamy in both sexes, and estimated that the proportion of sampled parents was 0.4 for each sex and genotyping error was set at 0.001 for each locus. We used COLONY output to quantify the number of offspring and partners per individual, without considering inferred parents.

(e) Reproductive success

To quantify individual reproductive success, we used samples collected in 2004 as our baseline adult generation because sampling in this year was systematic across the entire ecosystem, the number of loci genotyped was consistent (electronic supplementary material, table S1, more than 93% individuals had 24 markers genotyped), and because we had high probabilities of detecting their offspring in later years of sampling (2009–2012) based on age of primiparity. Female grizzly bears in the NCDE reach primiparity at a mean of 5.4 years old and average 2 cubs per litter, with each litter separated by approximately 3 years [47]. Male first age of reproduction can be as early as 4 years old, but can be later when older, more dominant males are present. Reproductive success refers only to the sampling period and incorporates individuals varying in age at the end of the study, and thus differs from lifetime reproductive success. We averaged the proportion of reproductively successful adult bears within each genetic neighbourhood based on a 33 km radius in a moving-window analysis (analogous to the above approach (sGD) used to calculate genetic diversity). We then compared results to weighted neighbourhood estimates of relative median density of male and female bears with original 10 km resolution [57].

(f) Low-diversity persistence and assimilation

We used spatial patterns in observed heterozygosity (H_0) from 2004 to identify peripheral regions in the NCDE where grizzly bears had low genetic diversity. Peripheral regions were bounded by selecting individuals with H_0 values less than 0.70, creating minimum convex polygons of individuals in each of the regions, and then buffering the polygons by 33 km to encompass individuals factoring into the low sGD estimates. To assess temporal changes in genetic diversity within the regions with low H_0 , we used the same boundaries and tracked changes in regional A_R , H_0 , H_E between time periods using the *diveRsity* package [58] for the R statistical environment [52]. We assessed significance of the difference across time in genetic metrics through bootstrap sampling of individuals within each region with 1000 replicates. Additionally, mean F_{IS} was calculated using 1000 bootstrap replicates. We then used patterns in individual reproductive success and dispersal to identify the demographic mechanisms potentially responsible for spatio-temporal patterns in genetic diversity (Objective 2).

Individuals within the buffered regions of low H_0 were classified as contemporary residents or immigrants (individuals dispersing from outside of the region). We used the mean location of mothers assigned in the parentage analysis as individual origins (i.e. locations of natal home ranges, as in [37,39,59]). When mothers were inferred and individuals were assigned fathers only, we used the mean location of the father as the origin. If no

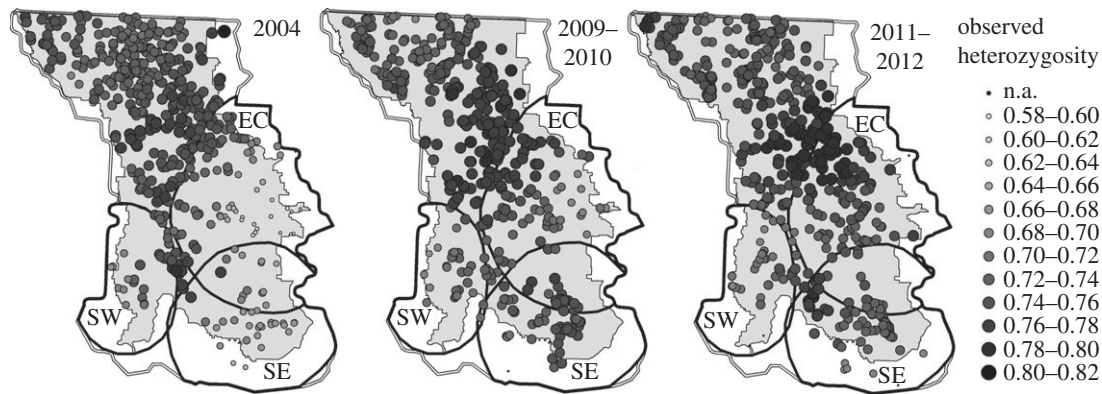


Figure 2. Observed heterozygosity (H_0) in the NCDE. Small, light-coloured circles represent low H_0 , while large, dark-coloured circles represent higher H_0 . Black polygons encompass regions of interest due to low H_0 in 2004. Small black dots indicate areas where individuals were detected but there were insufficient sample sizes ($n < 10$) to accurately calculate summary statistics.

parents were assigned, we had no information on origin location, and classified the individual as unknown. Individuals within each region that originated from outside of the region were classified as immigrants and individuals that had originated within the region were classified as residents unless they had descended from one of the identified immigrants, in which case they were classified as immigrant offspring or grandoffspring. Immigrants that originated from more than 66 km away from the region were additionally classified as long-distance migrants.

3. Results

(a) Spatial and temporal patterns in genetic diversity

Observed H_0 was relatively low in three regions of the NCDE in 2004; the southwest (SW), east-central (EC), and southeast (SE) (figure 2). In the SE, SW, and EC regions, we sampled 45, 28, and 98 different bears in 2004, 64, 32, and 104 bears in 2009–2010, and 72, 32, and 120 bears in 2011–2012. Five other measures of diversity: (i) the average number of alleles per locus (A), (ii) proportion of alleles in a genetic neighbourhood (A_P), (iii) allelic richness (A_R), (iv) Nei's genetic diversity (H_S), and (v) the inbreeding coefficient (F_{IS}) exhibit similar patterns of diversity as H_0 (electronic supplementary material, figures S2–S6). Varying the minimum number of neighbours and neighbourhood size had little effect on results.

(b) Reproductive success

The parentage analysis yielded 1287 assignments, including 435 triads (offspring with two assigned parents), 621 mother–offspring (M–O) dyads, and 666 father–offspring (F–O) dyads. Nearly all assignments contained zero mismatching loci, with eight assignments containing one mismatched loci, and one assignment containing two mismatched loci. Respectively, 205 and 139 unique mothers and fathers were identified from the full dataset.

Individual reproductive success varied greatly for both sexes (electronic supplementary material, figure S7a). Female reproductive success ranged from 0 offspring for nearly 50% of females up to 10 offspring for one individual in the SE, with a mean of 1.55 (median = 1). Male reproductive success ranged from 0 to 18 offspring with a mean of 2.06 (median = 0). Variability of success was substantial; over half of the males (59%) produced 0 detected offspring, while the

top four reproducers (located in the central and southern NCDE) fathered between 16 and 18 detected offspring each. A higher proportion of females (0.50) had reproductive success than did males (0.41) ($p = 0.03$, two sample test for equality of proportions).

There was a strong inverse relationship between bear density and the number of offspring per adult and the proportion of successful adults of both sexes. In the north part of the NCDE, bear density was highest and reproductive success was lowest (less than 40% of males with more than one offspring; electronic supplementary material, figure S8). In the lowest density areas, males produced an average of nearly twice as many detected offspring compared with males in high density areas (approx. 50% of males with more than or equal to one offspring), and females produced approximately 40% more offspring.

(c) Demographic mechanisms explaining patterns of genetic diversity

Several individuals with extremely high reproductive success had a large number of descendants in two of the three regions with relatively low genetic diversity (SE and SW), probably compounding the effects of contemporary and historical regional inbreeding associated with historical population decline and fragmentation. The relatively low genetic diversity in the SE region can be partially explained by the reproductive success of one individual. All of the SE residents (13 of 13) and nearly half of the individuals with unknown origins (8 of 18) detected in 2004 descend from one inferred male, and nearly all residents (11 of 13) also descended from one inferred female. The male fathered a highly productive male (8 offspring) and the two most productive females (10 and 8 offspring, respectively) in the entire ecosystem with two inferred females. The productive half-siblings (the male and females had the same father, but different mothers) also subsequently mated with each other, producing six offspring together. We sampled 101 descendants of the inferred male during the entire study period, primarily in the SE region (electronic supplementary material, figure S9b). The proportion of immigrants in the SE increased between 2004 and 2009–2010 samples (31–41%). This was largely due to an increase in the number of immigrant offspring between 2004, when three immigrant offspring were detected, and 2009–2010, when 10 immigrant offspring

Table 1. Number of immigrants into each region through time. Note that the same individual may be labelled as a migrant in multiple years. Long-distance migrants (LDM) are a subsample of immigrants in the region, not additional individuals.

	2004	2009–2010	2011–2012
southeast (SE) immigration			
class	total (LDM)	total (LDM)	total (LDM)
immigrants	11 (6)	16 (7)	22 (10)
immigrant offspring	3 (3)	10 (7)	4 (3)
immigrant grandoffspring	0 (0)	0 (0)	0 (0)
total immigrants in region	14 (9)	26 (14)	26 (13)
total bears sampled in region	45	64	72
percentage of region of immigrant origin	31.11% (20.00%)	40.63% (21.88%)	36.11% (18.06%)
southwest (SW) immigration			
immigrants	5 (1)	8 (3)	7 (2)
immigrant offspring	0 (0)	4 (1)	6 (0)
immigrant grandoffspring	0 (0)	0 (0)	0 (0)
total immigrants in region	5 (1)	12 (4)	13 (2)
total bears sampled in region	28	32	32
percentage of region of immigrant origin	17.86% (3.57%)	37.50% (12.50%)	40.63% (6.25%)
east-central (EC) immigration			
immigrants	27 (6)	30 (11)	41 (11)
immigrant offspring	7 (5)	14 (5)	14 (5)
immigrant grandoffspring	7 (3)	4 (3)	8 (4)
total immigrants in region	41 (14)	48 (19)	63 (20)
total bears sampled in region	98	104	120
percentage of region of immigrant origin	41.84% (14.29%)	46.15% (18.27%)	52.50% (16.67%)

were detected (table 1). This increase in immigrant reproductive success, as well as an increase in the number of bears detected, coincides with a significant increase in H_O (table 2) that continued through 2012 (2004 to 2009–2010 mean differences in $H_O = 0.06$ (lower 95% CI 0.00), 2004 to 2011–2012 mean differences in $H_O = 0.06$ (lower 95% CI 0.00)) and the erosion of the low diversity signature visible in 2004 in less than one generation (figure 2a–c).

In the SW region, one male dominated reproduction, siring 17 offspring, most of which dispersed only short distances (electronic supplementary material, figure S9a). Of those offspring, 14 descended from four females, three of which were three generations of a single family ('grandmother'–'daughter'–'granddaughter'). In 2004, the majority (10 of 16) of all residents sampled in the region were the offspring of this male. We detected 61 descendants of this male throughout the study. Dispersal into the region was substantial, and increased over time from a low of 5 in 2004 to 8 and 7 in 2009–2010 and 2011–2012, respectively, and included several immigrant offspring in the later sampling periods although not in 2004 (table 1). However, we identified only one long-distance disperser in each sampling period that did not come from one of the other two low diversity regions, and most immigrants were concentrated in the eastern side of the region. Despite increasing dispersal into the region, and a very slight increase in the number of bears detected, no significant difference in genetic diversity was observed over time (table 2).

The demographic processes underlying low initial diversity and subsequent increase in diversity in the EC region were more complicated than in the SE or SW. Despite low levels of H_O in 2004 (figure 2a), no sampled or inferred individuals contributed disproportionately to the local gene pool. In 2004, the individual with the most resident descendants in the region is the same inferred male that contributed disproportionately to the SE region (10 residents), while 10 immigrants in the region could be traced back to an individual detected far outside of the region which fathered two male immigrants, one of which was quite reproductively successful in the region (eight descendants). In 2004, we identified 27 immigrants, 7 immigrant offspring, and 7 immigrant grandoffspring (table 1). The presence of these immigrants and especially immigrant grandoffspring in 2004, which were not detected in either of the other two regions, suggests that dispersal into the EC began at least one or two generations prior to the other two regions. In spite of the large numbers of detected immigrants, genetic diversity was relatively low in 2004, suggesting that genetic diversity in this region may have been even lower in the past. H_O increased between 2004 and each of the latter two time periods, rising 0.05 (lower 95% CI 0.01) between 2004 and 2009–2010 and 0.07 (lower 95% CI 0.03) between 2004 and 2011–2012 (table 2). This also coincides with an increasing proportion of immigrants in the region, from 42% in 2004 to 46% in 2009–2010 and 53% in 2011–2012 (table 1). Levels of inbreeding (F_{IS}) in the EC were higher than expected under random mating

Table 2. Bootstrapped differences of genetic metrics through time within regions. Lower 95% confidence intervals not encompassing zero were considered significant differences between time periods.

region	allelic richness (A_R)		observed heterozygosity (H_O)		expected heterozygosity (H_E)	
	mean difference	lower 95% CI	mean difference	lower 95% CI	mean difference	lower 95% CI
EC 2004 to 2009–2010	0.05	–0.32	0.05	0.01	0.02	0.00
EC 2004 to 2011–2012	0.12	–0.25	0.07	0.03	0.03	0.01
EC 2009–2010 to 2011–2012	0.06	–0.25	0.02	–0.01	0.01	–0.01
SE 2004 to 2009–2010	0.25	–0.23	0.06	0.00	0.06	0.03
SE 2004 to 2011–2012	0.24	–0.16	0.06	0.00	0.06	0.02
SE 2009–2010 to 2011–2012	–0.01	–0.39	0.00	–0.04	–0.01	–0.03
SW 2004 to 2009–2010	0.19	–0.31	0.01	–0.06	0.00	–0.04
SW 2004 to 2011–2012	0.20	–0.27	0.00	–0.09	–0.01	–0.05
SW 2009–2010 to 2011–2012	0.01	–0.47	–0.02	–0.10	–0.01	–0.05
core (GNP) 2004 to 2009–2010	0.05	–0.19	0.01	–0.02	0.00	–0.01
core (GNP) 2004 to 2011–2012	0.15	–0.13	0.01	–0.02	0.00	–0.01
core (GNP) 2009–2010 to 2011–2012	0.10	–0.18	0.00	–0.04	0.00	–0.02

(i.e. there was a deficit of heterozygotes) in 2004 ($F_{IS} = 0.04$ (95% CI 0.00–0.09)), but had decreased by 2009–2010 ($F_{IS} = 0.00$ (95% CI –0.04–0.04)), and by 2011–2012, were lower still ($F_{IS} = -0.02$ (95% CI –0.06–0.02)); (electronic supplementary material, figure S5a–c and table S3).

4. Discussion

We used data from an extensive and rigorous ecosystem-scale genetic monitoring programme to demonstrate that genetic diversity in a large carnivore can be ephemeral and dynamic on the periphery of its range. Shifts in distribution, range expansions, and recolonizations primarily driven by climate change [60–62], species invasions [63], and more recently population growth of recovering species [64] are becoming increasingly ubiquitous for all biota, and increasingly complicated by the effects of habitat degradation and fragmentation [65–68]. Despite rapidly changing species distributions worldwide, our understanding of temporal patterns of genetic diversity in expanding populations is limited, and the underlying demographic mechanisms driving evolutionary changes at range margins have largely been ignored [69]. We found that idiosyncratic demographic processes consistently led to rapid local changes in genetic diversity in a recovering carnivore found across northern latitudes.

Range contraction and habitat fragmentation of NCDE grizzly bears occurred for approximately a century, with the population reaching a low point in the 1920s or 1930s [45]. The protracted reduction in the population probably caused the reduced genetic diversity found in peripheral remnant groups at the beginning of this study, as expected when lengthy range contractions occur [70]. In this system, the effects of over 10 generations of semi-isolation and reproductive bottlenecks, common to small populations of carnivores globally [27,71–73], were erased via an influx of immigrants as the core population underwent range expansion. Our

study supports the importance of dispersal and connectivity in facilitating range expansions and restoring genetic diversity [74–78] by empirically demonstrating that high landscape permeability coupled with the intrinsic dispersal capacity of large carnivores [79] can lead to rapid restoration of genetic diversity in species of conservation concern.

The small size and isolation of animals living on the range periphery often predispose remnant groups to lower genetic diversity due to reduced gene flow [80] and smaller effective population sizes [81]. In early years of the study, we found relatively few immigrants entering the peripheral regions and highly skewed reproductive success among individuals, with several individuals dominating reproduction. Over less than a single generation, two of the three remnant groups showed significant increases in H_O , a pattern consistent with expectations of extreme temporal variation on the range periphery [81]. The increases of H_O in the SE and EC periphery were six and seven times the magnitude of genetic change in the core over the same period of time, respectively. The increase of genetic diversity occurred in conjunction with an influx of immigrants and a surge of successful breeders. Despite the significant increase in genetic diversity, nearly all (37/45–82%) of the southernmost females detected in the SE periphery descended from three females, illustrating a trend that is likely to continue at the expansion front due to male-biased dispersal of grizzly bears [39,59,82]. A similar pattern is likely for many mammals owing to their tendency for male-biased dispersal [83], where persistently female relatedness may exist despite increases in overall genetic diversity within populations.

The evolutionary dynamics on the expansion front of a species' range has been a major focus of both theoretical and empirical studies. Theoretical studies have focused primarily on the patterns of colonization during range expansion in the absence of existing remnant groups (e.g. [7,11]), and the influence dispersal has on those patterns [8]. Similarly, empirical studies have focused on genetic drift

and adaptive dynamics along the expansion axis (e.g. [84,85]). Edge populations may be particularly important sources of genetic diversity that may enable species persistence particularly in changing environments [80,81]. However, the transient nature of genetic diversity at range margins [81] greatly complicates conservation efforts that focus on protecting genetic diversity or understanding patterns of connectivity (i.e. landscape genetics; [86]) based on data with restricted spatial or temporal replication. Ultimately, the data presented here highlight that a broad spatial and temporal perspective is necessary for understanding evolutionary dynamics at the edge of species distributions where adaptive and stochastic dynamics may be at their strongest.

The patterns in genetic diversity caused by the assimilation of existing remnant groups by a core population range expansion (reduced genetic diversity in peripheral groups, founder effects, etc.) closely resemble the outcome of a pure range expansion (e.g. [87]). However, they are in fact the product of both a prolonged contraction and a subsequent recolonization. Interestingly, populations resulting from the two distinct processes may be adaptively and demographically very different. Considering the prevalence of remnant groups in carnivore populations around the world [19–29], the ongoing recovery of many populations [64], and the increasing probability of range shifts, contractions and expansions related to climate change, we expect that neutral and adaptive evolutionary changes caused by recolonization and assimilation will be increasingly common.

Patterns of genetic diversity in populations are dynamic in space and time, particularly for species undergoing changes in population dynamics and geographical distributions. Extreme changes can occur in less than a single generation and are surprisingly idiosyncratic and stochastic.

Individual-level, local demography, an oft-neglected driver of contemporary evolutionary dynamics plays a critical role in shaping patterns of genetic diversity, although the overall trajectory is influenced by historical events (e.g. inbreeding, isolation, and random genetic drift) and also contemporary gene flow (e.g. dispersal). As such, we suggest caution when making landscape-scale conservation and management decisions based on a single sampling snapshot in time. Long-term, ecosystem-scale monitoring of focal populations illuminate processes that govern spatial and temporal patterns in ecological and evolutionary dynamics, providing key insights that might otherwise be missed.

Data accessibility. The genetic profiles have been deposited in Science-Base and are freely available.

Authors' contributions. N.M., T.A.G., and R.K. designed the study and analysis. N.M. performed the analyses. K.C.K., A.C.M., T.A.G., and many others painstakingly collected the data. All authors contributed to the writing of the manuscript.

Competing interests. We have no competing interests.

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References

- Ceballos G, Ehrlich PR. 2002 Mammal population losses and the extinction crisis. *Science* **296**, 904–907. (doi:10.1126/science.1069349)
- Laliberte AS, Ripple WJ. 2004 Range contractions of North American carnivores and ungulates. *Bioscience* **54**, 123–138. (doi:10.1641/0006-3568(2004)054[0123:rconac]2.0.co;2)
- Morrison JC, Sechrest W, Dinerstein E, Wilcove DS, Lamoreux JF. 2007 Persistence of large mammal faunas as indicators of global human impacts. *J. Mamm.* **88**, 1363–1380. (doi:10.1644/06-mamm-a-124r2.1)
- Proctor MF, McLellan BN, Strobeck C, Barclay RMR. 2005 Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proc. R. Soc. B* **272**, 2409–2416. (doi:10.1098/rspb.2005.3246)
- Ripple WJ *et al.* 2014 Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484. (doi:10.1126/science.1241484)
- Soule ME. 1985 What is conservation biology. *Bioscience* **35**, 727–734. (doi:10.2307/1310054)
- Austerlitz F, JungMuller B, Godelle B, Gouyon PH. 1997 Evolution of coalescence times, genetic diversity and structure during colonization. *Theor. Popul. Biol.* **51**, 148–164. (doi:10.1006/tpbi.1997.1302)
- Excoffier L, Foll M, Petit RJ. 2009 Genetic consequences of range expansions. *Annu. Rev. Ecol. Syst.* **40**, 481–501. (doi:10.1146/annurev.ecolsys.39.110707.173414)
- Excoffier L, Ray N. 2008 Surfing during population expansions promotes genetic revolutions and structuration. *Trends Ecol. Evol.* **23**, 347–351. (doi:10.1016/j.tree.2008.04.004)
- Ibrahim KM, Nichols RA, Hewitt GM. 1996 Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. *Heredity* **77**, 282–291. (doi:10.1038/hdy.1996.142ER)
- Le Corre V, Kremer A. 1998 Cumulative effects of founding events during colonisation on genetic diversity and differentiation in an island and stepping-stone model. *J. Evol. Biol.* **11**, 495–512. (doi:10.1007/s000360050102)
- Peischl S, Dupanloup I, Kirkpatrick M, Excoffier L. 2013 On the accumulation of deleterious mutations during range expansions. *Mol. Ecol.* **22**, 5972–5982. (doi:10.1111/mec.12524)
- Slatkin M, Excoffier L. 2012 Serial founder effects during range expansion: a spatial analog of genetic drift. *Genetics* **191**, 171–181. (doi:10.1534/genetics.112.139022)
- Arenas M, Francois O, Currat M, Ray N, Excoffier L. 2013 Influence of admixture and paleolithic range contractions on current european diversity gradients. *Mol. Biol. Evol.* **30**, 57–61. (doi:10.1093/molbev/mss203)
- Hewitt G. 2000 The genetic legacy of the Quaternary ice ages. *Nature* **405**, 907–913. (doi:10.1038/35016000)
- Hewitt GM. 1996 Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* **58**, 247–276. (doi:10.1111/j.1095-8312.1996.tb01434.x)
- Hirata D *et al.* 2013 Molecular phylogeography of the brown bear (*Ursus arctos*) in Northeastern Asia based on analyses of complete mitochondrial DNA

- sequences. *Mol. Biol. Evol.* **30**, 1644–1652. (doi:10.1093/molbev/mst077)
18. Ramakrishnan AP, Musial T, Cruzan MB. 2010 Shifting dispersal modes at an expanding species' range margin. *Mol. Ecol.* **19**, 1134–1146. (doi:10.1111/j.1365-294X.2010.04543.x)
 19. Cegelski CC, Waits LP, Anderson NJ. 2003 Assessing population structure and gene flow in Montana wolverines (*Gulo gulo*) using assignment-based approaches. *Mol. Ecol.* **12**, 2907–2918. (doi:10.1046/j.1365-294X.2003.01969.x)
 20. Ciucci P, Gervasi V, Boitani L, Boulanger J, Paetkau D, Prive R, Tosoni E. 2015 Estimating abundance of the remnant Apennine brown bear population using multiple noninvasive genetic data sources. *J. Mamm.* **96**, 206–220. (doi:10.1093/jmammal/gyu029)
 21. Clevenger AP, Purroy FJ, Campos MA. 1997 Habitat assessment of a relict brown bear *Ursus arctos* population in northern Spain. *Biol. Conserv.* **80**, 17–22. (doi:10.1016/S0006-3207(96)00081-x)
 22. Darimont CT, Paquet PC. 2002 The gray wolves, *Canis lupus*, of British Columbia's central and north coast: distribution and conservation assessment. *Can. Field Nat.* **116**, 416–422.
 23. Doko T, Fukui H, Kooiman A, Toxopeus AG, Ichinose T, Chen W, Skidmore AK. 2011 Identifying habitat patches and potential ecological corridors for remnant Asiatic black bear (*Ursus thibetanus japonicus*) populations in Japan. *Ecol. Modell.* **222**, 748–761. (doi:10.1016/j.ecolmodel.2010.11.005)
 24. Gil-Sanchez JM, Ballesteros-Duperon E, Bueno-Segura JF. 2006 Feeding ecology of the Iberian lynx *Lynx pardinus* in eastern Sierra Morena (Southern Spain). *Acta Theriologica* **51**, 85–90. (doi:10.1007/bf03192659)
 25. Kyle CJ, Strobeck C. 2001 Genetic structure of North American wolverine (*Gulo gulo*) populations. *Mol. Ecol.* **10**, 337–347. (doi:10.1046/j.1365-294X.2001.01222.x)
 26. Miotto RA, Cervini M, Figueiredo MG, Begotti RA, Galetti PM. 2011 Genetic diversity and population structure of pumas (*Puma concolor*) in southeastern Brazil: implications for conservation in a human-dominated landscape. *Conserv. Genet.* **12**, 1447–1455. (doi:10.1007/s10592-011-0243-8)
 27. Straka M, Paule I, Ionescu O, Stofik J, Adamec M. 2012 Microsatellite diversity and structure of Carpathian brown bears (*Ursus arctos*): consequences of human caused fragmentation. *Conserv. Genet.* **13**, 153–164. (doi:10.1007/s10592-011-0271-4)
 28. van Gils H, Westinga E, Carafa M, Antonucci A, Ciaschetti G. 2014 Where the bears roam in Majella National Park, Italy. *J. Nat. Conserv.* **22**, 23–34. (doi:10.1016/j.jnc.2013.08.001)
 29. Weckworth BV, Talbot SL, Cook JA. 2010 Phylogeography of wolves (*Canis lupus*) in the Pacific Northwest. *J. Mamm.* **91**, 363–375. (doi:10.1644/09-mamm-a-036.1)
 30. Stirling I, Derocher AE. 2012 Effects of climate warming on polar bears: a review of the evidence. *Glob. Change Biol.* **18**, 2694–2706. (doi:10.1111/j.1365-2486.2012.02753.x)
 31. Castilho CS, Marins-Sa LG, Benedet RC, Freitas TO. 2011 Landscape genetics of mountain lions (*Puma concolor*) in southern Brazil. *Mamm. Biol.* **76**, 476–483. (doi:10.1016/j.mambio.2010.08.002)
 32. Costello CM, Creel SR, Kalinowski ST, Vu NV, Quigley HB. 2009 Determinants of male reproductive success in American black bears. *Behav. Ecol. Sociobiol.* **64**, 125–134. (doi:10.1007/s00265-009-0828-0)
 33. De Barba M, Waits LP, Garton EO, Genovesi P, Randi E, Mustoni A, Groff C. 2010 The power of genetic monitoring for studying demography, ecology and genetics of a reintroduced brown bear population. *Mol. Ecol.* **19**, 3938–3951. (doi:10.1111/j.1365-294X.2010.04791.x)
 34. Frosch C, Dutsov A, Zlatanova D, Valchev K, Reiners TE, Steyer K, Pfenninger M, Nowak C. 2014 Noninvasive genetic assessment of brown bear population structure in Bulgarian mountain regions. *Mamm. Biol.* **79**, 268–276. (doi:10.1016/j.mambio.2014.04.001)
 35. Hedmark E, Ellegren H. 2007 DNA-based monitoring of two newly founded Scandinavian wolverine populations. *Conserv. Genet.* **8**, 843–852. (doi:10.1007/s10592-006-9231-9)
 36. Itoh T, Sato Y, Kobayashi K, Mano T, Iwata R. 2012 Effective dispersal of brown bears (*Ursus arctos*) in eastern Hokkaido, inferred from analyses of mitochondrial DNA and microsatellites. *Mamm. Study* **37**, 29–41. (doi:10.3106/041.037.0104)
 37. Moore JA, Draheim HM, Etter D, Winterstein S, Scribner KT. 2014 Application of large-scale parentage analysis for investigating natal dispersal in highly vagile vertebrates: a case study of American black bears (*Ursus americanus*). *PLoS ONE* **9**, e91168. (doi:10.1371/journal.pone.0091168)
 38. Moore JA, Xu R, Frank K, Draheim H, Scribner KT. 2015 Social network analysis of mating patterns in American black bears (*Ursus americanus*). *Mol. Ecol.* **24**, 4010–4022. (doi:10.1111/mec.13290)
 39. Proctor MF, McLellan BN, Strobeck C, Barclay RMR. 2004 Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Can. J. Zool.* **82**, 1108–1118. (doi:10.1139/z04-077)
 40. Sawaya MA, Kalinowski ST, Clevenger AP. 2014 Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. *Proc. R. Soc. B* **281**, 20131705. (doi:10.1098/rspb.2013.1705)
 41. Van Horn RC, Engh AL, Scribner KT, Funk SM, Holekamp KE. 2004 Behavioural structuring of relatedness in the spotted hyena (*Crocuta crocuta*) suggests direct fitness benefits of clan-level cooperation. *Mol. Ecol.* **13**, 449–458. (doi:10.1046/j.1365-294X.2003.02071.x)
 42. U.S. Fish and Wildlife Service [USFWS]. 2011 Grizzly bear (*Ursus arctos horribilis*) 5-year review: summary and evaluation, 205. Missoula, MT: U.S. Fish and Wildlife Service, Grizzly Bear Recovery Office.
 43. Proctor MF *et al.* 2012 Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildl. Monogr.* **180**, 1–46. (doi:10.1002/wmon.6)
 44. Kendall KC *et al.* 2015 Density, distribution, and genetic structure of grizzly bears in the Cabinet-Yaak Ecosystem. *J. Wildl. Manage.* **80**, 314–331. (doi:10.1002/jwmg.1019)
 45. U.S. Fish and Wildlife Service [USFWS]. 1993 Grizzly bear recovery plan. Missoula, MT: U.S. Fish Wildlife Service.
 46. Kendall KC, Stetz JB, Boulanger J, Macleod AC, Paetkau D, White GC. 2009 Demography and genetic structure of a recovering grizzly bear population. *J. Wildl. Manage.* **73**, 3–17. (doi:10.2193/2008-330)
 47. Mace RD *et al.* 2012 Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. *J. Wildl. Manage.* **76**, 119–128. (doi:10.1002/jwmg.250)
 48. Kamath PL, Haroldson MA, Luikart G, Paetkau D, Whitman C, Van Manen FT. 2015 Multiple estimates of effective population size for monitoring a long-lived vertebrate: an application to Yellowstone grizzly bears. *Mol. Ecol.* **24**, 5507–5521. (doi:10.1111/mec.13398)
 49. Ennis S, Gallagher TF. 1994 A PCR-based sex-determination assay in cattle based on the bovine amelogenin locus. *Anim. Genet.* **25**, 425–427. (doi:10.1111/j.1365-2052.1994.tb00533.x)
 50. Peakall R, Smouse PE. 2012 GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* **28**, 2537–2539. (doi:10.1093/bioinformatics/bts460)
 51. Shirk AJ. 2014 sGD: spatially explicit estimation of genetic diversity indices and Wright's neighborhood size (NS). R package version 2.0. 2008/73, 158–70. (doi:10.3389/fevo.2014.00062)
 52. R Core Team. 2015 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org/>.
 53. Jones OR, Wang JL. 2010 COLONY: a program for parentage and sibship inference from multilocus genotype data. *Mol. Ecol. Resources* **10**, 551–555. (doi:10.1111/j.1755-0998.2009.02787.x)
 54. Wang JL. 2004 Sibship reconstruction from genetic data with typing errors. *Genetics* **166**, 1963–1979. (doi:10.1534/genetics.166.4.1963)
 55. Wang JL, Santure AW. 2009 Parentage and sibship inference from multilocus genotype data under polygamy. *Genetics* **181**, 1579–1594. (doi:10.1534/genetics.108.100214)
 56. Harrison HB, Saenz-Agudelo P, Planes S, Jones GP, Berumen ML. 2013 Relative accuracy of three common methods of parentage analysis in natural populations. *Mol. Ecol.* **22**, 1158–1170. (doi:10.1111/mec.12138)
 57. Graves TA, Royle JA, Kendall KC, Beier P, Stetz JB, Macleod AC. 2012 Balancing Precision and Risk: Should Multiple Detection Methods Be Analyzed Separately in N-Mixture Models? *PLoS ONE* **7**(12). (doi:10.1371/journal.pone.0049410)
 58. Keenan K, McGinnity P, Cross TF, Crozier WW, Prodöhl PA. 2013 diveRcity: an R package for the

- estimation of population genetics parameters and their associated errors. *Methods Ecol. Evol.* **4**, 782–788. (doi:10.1111/2041-210X.12067)
59. Graves T, Chandler RB, Royle JA, Beier P, Kendall KC. 2014 Estimating landscape resistance to dispersal. *Landscape Ecol.* **29**, 1201–1211. (doi:10.1007/s10980-014-0056-5)
 60. Chen IC, Hill JK, Ohlemueller R, Roy DB, Thomas CD. 2011 Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026. (doi:10.1126/science.1206432)
 61. Parmesan C, Yohe G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
 62. Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60. (doi:10.1038/nature01333)
 63. Simberloff D *et al.* 2013 Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* **28**, 58–66. (doi:10.1016/j.tree.2012.07.013)
 64. Crooks KR, Burdett CL, Theobald DM, Rondinini C, Boitani L. 2011 Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Phil. Trans. R. Soc. B* **366**, 2642–2651. (doi:10.1098/rstb.2011.0120)
 65. Hodgson JA, Thomas CD, Dytham C, Travis MJ, Cornell SJ. 2012 The speed of range shifts in fragmented landscapes. *PLoS ONE* **7**, e47141. (doi:10.1371/journal.pone.0047141)
 66. Honnay O, Verheyen K, Butaye J, Jacquemyn H, Bossuyt B, Hermy M. 2002 Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecol. Lett.* **5**, 525–530. (doi:10.1046/j.1461-0248.2002.00346.x)
 67. Opdam P, Wascher D. 2004 Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* **117**, 285–297. (doi:10.1016/j.biocon.2003.12.008)
 68. Eckert CG, Samis KE, Loughheed SC. 2008 Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol. Ecol.* **17**, 1170–1188. (doi:10.1111/j.1365-294X.2007.03659.x)
 69. Arenas M, Ray N, Currat M, Excoffier L. 2012 Consequences of range contractions and range shifts on molecular diversity. *Mol. Biol. Evol.* **29**, 207–218. (doi:10.1093/molbev/msr187)
 70. Aspi J, Roininen E, Ruokonen M, Kojola I, Vila C. 2006 Genetic diversity, population structure, effective population size and demographic history of the Finnish wolf population. *Mol. Ecol.* **15**, 1561–1576. (doi:10.1111/j.1365-294X.2006.02877.x)
 71. Jones ME, Paetkau D, Geffen E, Moritz C. 2004 Genetic diversity and population structure of Tasmanian devils, the largest marsupial carnivore. *Mol. Ecol.* **13**, 2197–2209. (doi:10.1111/j.1365-294X.2004.02239.x)
 72. Wisely SM, Buskirk SW, Fleming MA, McDonald DB, Ostrander EA. 2002 Genetic diversity and fitness in black-footed ferrets before and during a bottleneck. *J. Heredity* **93**, 231–237. (doi:10.1093/jhered/93.4.231)
 73. Keller LF, Waller DM. 2002 Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**, 230–241. (doi:10.1016/s0169-5347(02)02489-8)
 74. McEachern MB, Van Vuren DH, Floyd CH, May B, Eadie JM. 2011 Bottlenecks and rescue effects in a fluctuating population of golden-mantled ground squirrels (*Spermophilus lateralis*). *Conserv. Genet.* **12**, 285–296. (doi:10.1007/s10592-010-0139-z)
 75. Beier P, Brost B. 2010 Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conserv. Biol.* **24**, 701–710. (doi:10.1111/j.1523-1739.2009.01422.x)
 76. Vila C *et al.* 2003 Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proc. R. Soc. Lond. B* **270**, 91–97. (doi:10.1098/rspb.2002.2184)
 77. Zgurski JM, Hik DS. 2014 Gene flow and the restoration of genetic diversity in a fluctuating collared pika (*Ochotona collaris*) population. *Conserv. Genet.* **15**, 37–48. (doi:10.1007/s10592-013-0519-2)
 78. Schloss CA, Nunez TA, Lawler JJ. 2012 Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl Acad. Sci. USA* **109**, 8606–8611. (doi:10.1073/pnas.1116791109)
 79. Lesica P, Allendorf FW. 1995 When are peripheral populations valuable for conservation? *Conserv. Biol.* **9**, 753–760. (doi:10.1046/j.1523-1739.1995.09040753.x)
 80. Vucetich JA, Waite TA. 2003 Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. *Conserv. Genet.* **4**, 639–645. (doi:10.1023/a:1025671831349)
 81. McLellan BN, Hovey FW. 2001 Natal dispersal of grizzly bears. *Can. J. Zool.* **79**, 838–844. (doi:10.1139/cjz-79-5-838)
 82. Dobson FS. 1982 Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* **30**, 1183–1192. (doi:10.1016/S0003-3472(82)80209-1)
 83. Buckley J, Butlin RK, Bridle JR. 2012 Evidence for evolutionary change associated with the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate change. *Mol. Ecol.* **21**, 267–280. (doi:10.1111/j.1365-294X.2011.05388.x)
 84. White TA, Perkins SE, Heckel G, Searle JB. 2013 Adaptive evolution during an ongoing range expansion: the invasive bank vole (*Myodes glareolus*) in Ireland. *Mol. Ecol.* **22**, 2971–2985. (doi:10.1111/mec.12343)
 85. Manel S, Schwartz MK, Luikart G, Taberlet P. 2003 Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* **18**, 189–197. (doi:10.1016/s0169-5347(03)00008-9)
 86. Chapron G *et al.* 2014 Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* **346**, 1517–1519. (doi:10.1126/science.1257553)
 87. Hagen SB, Kopatz A, Aspi J, Kojola I, Eiken HG. 2015 Evidence of rapid change in genetic structure and diversity during range expansion in a recovering large terrestrial carnivore. *Proc. R. Soc. B* **282**, 20150092. (doi:10.1098/rspb.2015.0092)