Journal of Animal Ecology

BRITISH ECOLOGICAL SOCIETY

*Journal of Animal Ecology* 2017, **86,** 55–65 doi: 10.1111/1365-2656.12589

# 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; Dwernychuk & 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

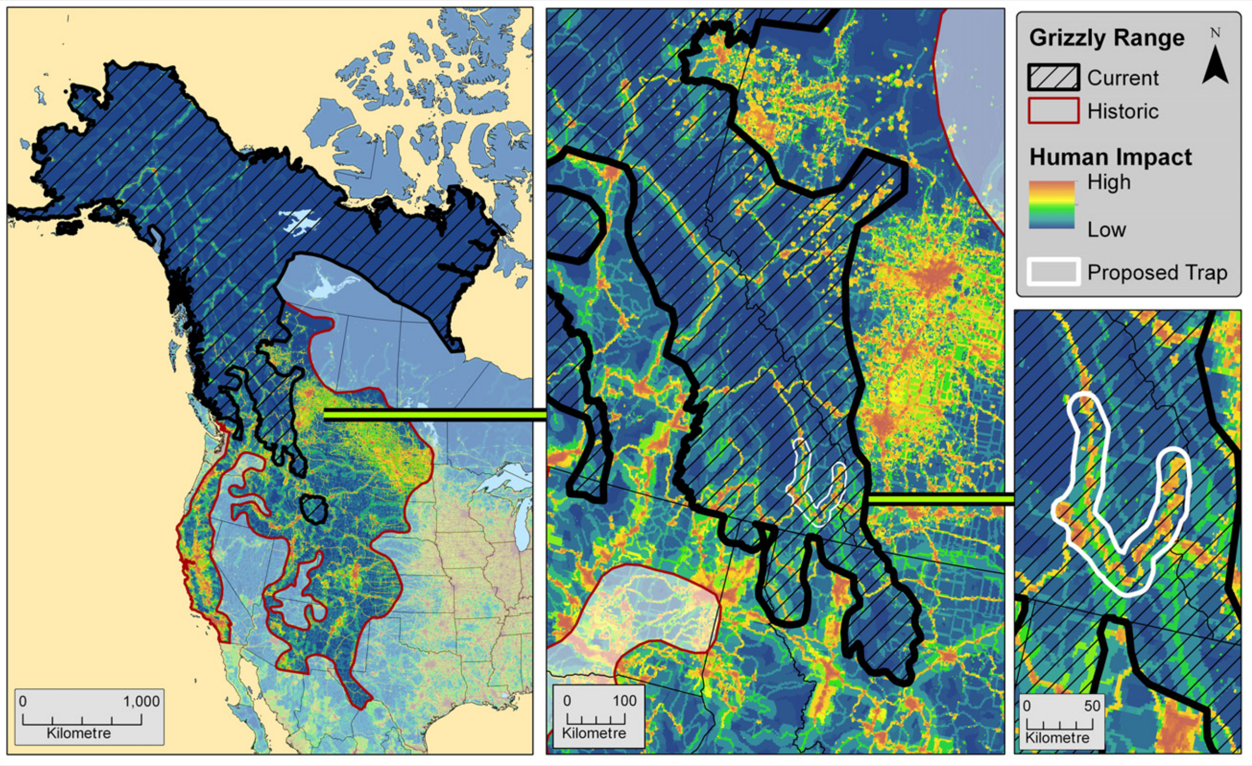

**Fig. 1.** Current and historical distribution of grizzly bears across North America (left) with Human Influence Index shown from high to low influence (HII, Wildlife Conservation Society – WCS, and Center for International Earth Science Information Network – CIESIN – Columbia University 2005). Middle: 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 km$^2$ 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.

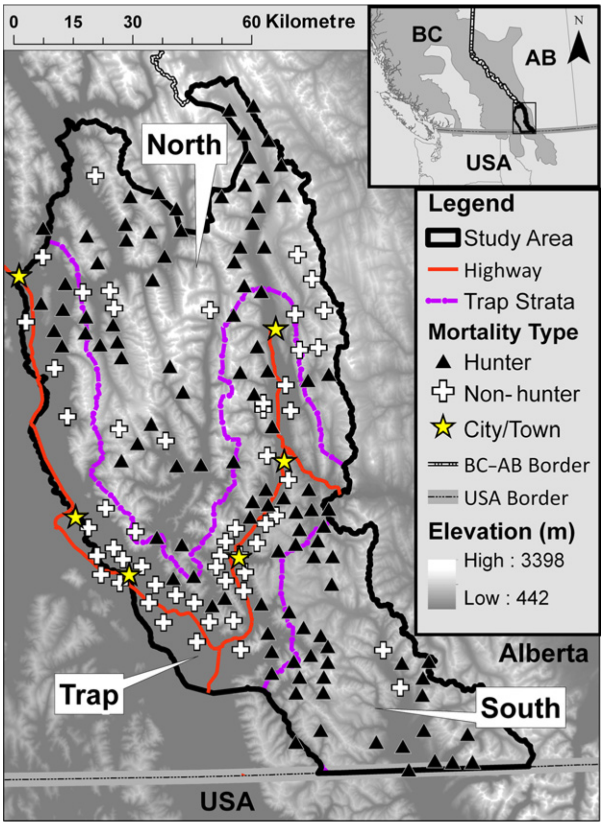

**Fig. 2.** Study area for the South Rockies Grizzly Bear Project, and locations of all recorded human-caused grizzly bear mortalities between 2006 and 2014 in south-east British Columbia, Canada. The Trap stratum buffers the highway (red line) and is shown as the polygon enclosed by the thick purple 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 km$^2$ 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 ($\pm$6·8) and *M*: 15 ($\pm$2·7)/1000 km$^2$; 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 ($\phi$), apparent recruitment ($f$), realized population growth ($\lambda$), 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 ($\lambda$) is simply the sum of the probability of entering the population [apparent recruitment ($f$)] and the probability of remaining in the population [apparent survival ($\phi$)] (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 km$^2$ per bear) than the North (7·0 km$^2$ per bear) or South (9·3 km$^2$ 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 ± SE = 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 ($P \leq 0{\cdot}0001$ between all strata except North–South where $P = 0{\cdot}91$, Fig. 3d). Estimated apparent survival rates were lower in the Trap ($\phi = 0{\cdot}65 \pm \mathrm{SE} = 0{\cdot}053$) than in surrounding areas (North $\phi = 0{\cdot}79 \pm 0{\cdot}020$, and South $\phi = 0{\cdot}78 \pm 0{\cdot}037$), and also differed statistically in Trap–North and Trap–South comparisons ($P \leq 0{\cdot}05$) but not in North–South comparisons ($P = 0{\cdot}79$) (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 ($f = 0{\cdot}27 \pm \mathrm{SE} = 0{\cdot}058$), which was marginally higher than in the North ($f = 0{\cdot}16 \pm 0{\cdot}023$, $P = 0{\cdot}09$), but not higher than in the South ($f = 0{\cdot}19 \pm 0{\cdot}038$, $P = 0{\cdot}25$, Fig. 3c), with no statistical significant difference detected between the North and South ($P > 0{\cdot}56$). All strata demonstrated annual growth rates below 1: Trap = 0·92 ± SE = 0·040, North = 0·95 ± 0·023 and South = 0·97 ± 0·037, $P > 0{\cdot}05$ 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) ($P = 0{\cdot}003$, 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 ($P < 0{\cdot}01$) 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 ($P = 0{\cdot}99$) or between sexes ($P = 0{\cdot}56$).

Average annual sex ratio in the Trap was 1·17 (±SE = 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 ($P = 0{\cdot}02$), but not between the South and Trap ($P = 0{\cdot}13$) or the North and South ($P = 0{\cdot}07$). 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

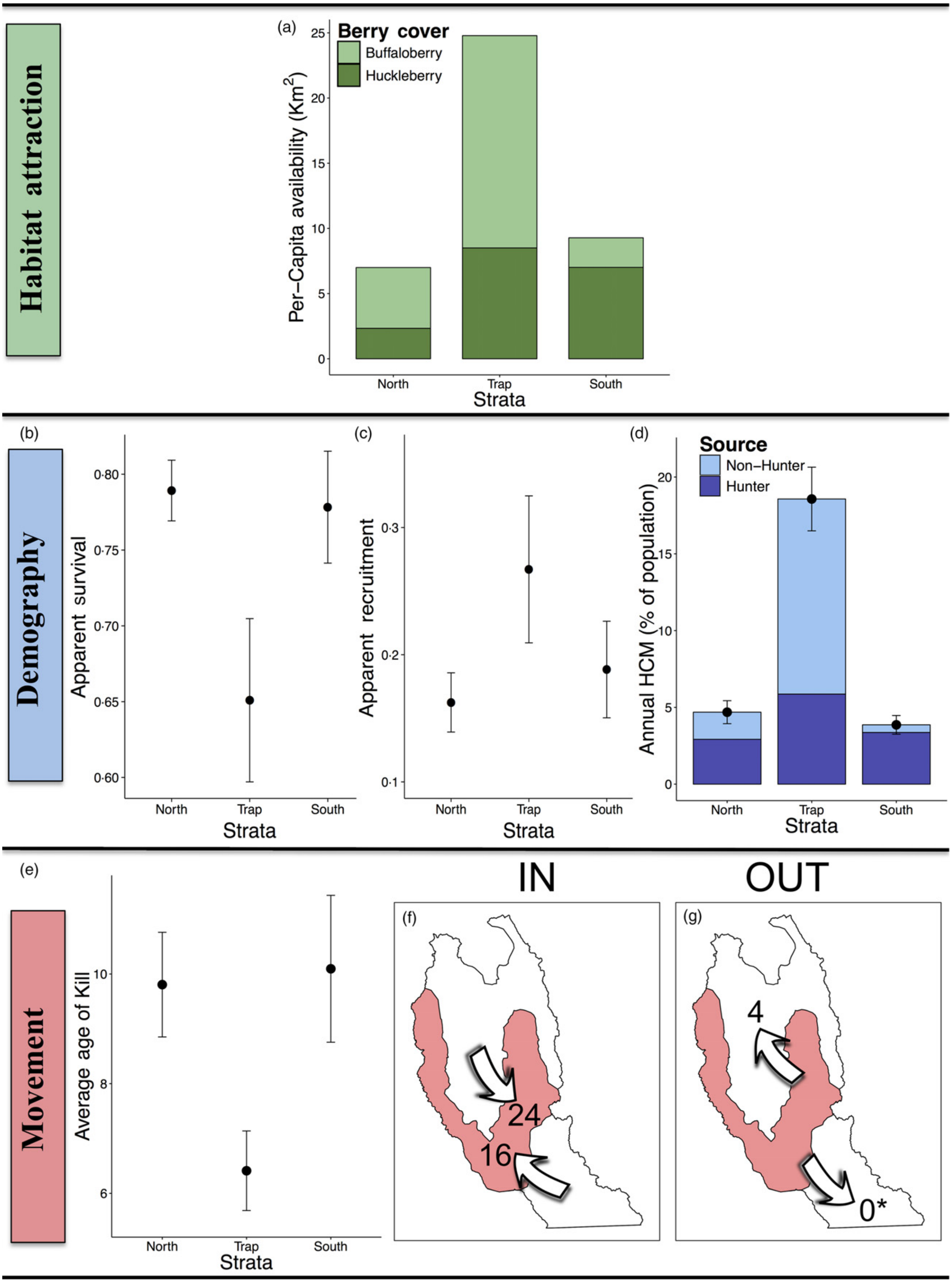
Habitat attraction
(a)
Berry cover
Buffaloberry
Huckleberry
Per–Capita availability (Km$^2$)
0
5
10
15
20
25
North
Trap
South
Strata
Demography
(b)
Apparent survival
0·60
0·65
0·70
0·75
0·80
North
Trap
South
Strata
(c)
Apparent recruitment
0·1
0·2
0·3
North
Trap
South
Strata
(d)
Source
Non–Hunter
Hunter
Annual HCM (% of population)
0
5
10
15
20
North
Trap
South
Strata
Movement
(e)
Average age of Kill
6
8
10
North
Trap
South
Strata
IN
OUT
(f)
24
16
(g)
4
0*

**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 km$^2$. *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 ($P < 0{\cdot}001$).

## 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 km$^2$ (Mowat *et al.* 2013), much higher than we found a decade later (18·5/1000 km$^2$). Projecting the 2002/2003 density through time using the growth rate estimated here for the Trap ($\lambda = 0{\cdot}92$) to the median year of this study suggests a density similar to our estimated density (density projected = 18·7/1000 km$^2$). 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 buffaloberry 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, Treml & 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.

## Acknowledgements

We thank the many people who helped collect these data and Eric Nielsen, Sophie Gilbert, Craig Demars, Michael Proctor and Laura Smit for insightful comments on this work. We are indebted to Deborah MacKillop and Deepa Filatow for providing data to complete our fruit models. Thanks to Bill and Sue Hanlon for providing logistical support in the field. The Natural Science and Engineering Research Council of Canada, Vanier Canada Graduate Scholarships, Ministry of Forests, Lands and Natural Resource Operations, Habitat Conservation Trust Fund, Safari Club International, Columbia Basin Trust Fund, BP Canada, and BC Conservation Corps graciously provided funding for this work. We thank two anonymous reviewers for improving this manuscript considerably. The authors of this work have no competing interests to disclose.

## Data accessibility

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

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*Received 30 April 2016; accepted 10 August 2016*
*Handling Editor: Jean-Michel Gaillard*

## 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.