



# Linking habitat use to mortality and population viability to disarm an ecological trap

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## ABSTRACT

Animal excursions out of protected areas are a source of human-wildlife conflict and can lead animals into ecological traps. These arise when animals prefer areas of their habitat conferring lower fitness than other available areas. Ecological traps should become increasingly common as humans continue to alter habitats, yet their impact on population viability has rarely been documented and there is limited knowledge on how to disarm them. Moreover, although spatial factors such as the proportion of trap habitat in the landscape are crucial in determining the probability of extinction, few studies have attempted to link animal use of space to demography to obtain insights into how to release trapped populations. Here we tackle these gaps using a stochastic, spatially explicit matrix model parametrized with empirical data. We show that a free-ranging population of plains bison (*Bison bison bison*) caught in an ecological trap caused by legal but unregulated hunting has a 66% probability of extinction over the next 50 years under current conditions. By linking the time bison spent in fields with hunting permission to survival and population persistence, we show that bison use of such fields must decrease by 70% to ensure population viability. Our approach narrowed down the ecological trap to < 1% of the population's range during the hunting period. Targeting this limited portion of the landscape would hence be a cost-effective strategy to disarm the trap. We show that a spatially explicit approach to demography can refine conservation strategies to avoid potentially onerous and ineffective interventions.

## 1. Introduction

Excursions by terrestrial vertebrates out of protected areas and into habitat strongly impacted by human activity are a major source of human-wildlife conflict across the globe and one of the main challenges in contemporary wildlife management (Goswami et al., 2014; Williams et al., 2017; Torres et al., 2018; van Eeden et al., 2018). In some cases, such excursions can lead wildlife into ecological traps, a situation in which animals prefer areas of their habitat conferring lower fitness than other available areas (Schlaepfer et al., 2002; Robertson and Hutto, 2006). Ecological traps usually arise as a result of human-induced rapid environmental change, which shift environmental conditions at a faster rate than wildlife can adapt (Battin, 2004; Robertson et al., 2013; Sih, 2013).

Animals are misled into maladaptive habitat selection because of a decoupling between the environmental cue they use to assess habitat quality and the actual fitness value of using an area (Robertson et al., 2013; Hale and Swearer, 2016). For instance, plains bison (*Bison bison*)

occupying the interface of a protected area and a rural landscape select agricultural fields as forage patches but incur increased mortality by humans in these areas with no perceptible gains in reproduction (Sigaud et al., 2017). The environmental cue that bison use to evaluate the quality of food patches is the profitability (i.e. the ratio between digestible energy and handling time) of forage (Babin et al., 2011; Merkle et al., 2014). Accordingly, bison select agricultural fields when crops become more profitable than the natural forage available in the protected area; in doing so, however, they expose themselves to unregulated hunting by humans (Sigaud et al., 2017). Bison abundance in this population has declined by about 50% in less than a decade as selection for agricultural fields increased (Sigaud et al., 2017). Harvesting by humans is a known factor capable of creating ecological traps (Abrams et al., 2012), and examples of other animals caught in traps caused by human-induced mortality at the boundary of protected areas include leopards *Panthera pardus* (Balme et al., 2010), Andean bears *Tremarctos ornatus* (Sanchez-Mercado et al., 2014) and African wild dogs *Lycan pictus* (van der Meer et al., 2014).

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Ecological traps are expected to become increasingly common as humans continue to alter the environmental conditions faced by animals (Battin, 2004; Sih, 2013), and several simulation studies have demonstrated that traps can lead to local population and even metapopulation extinction (Delibes et al., 2001; Donovan and Thompson, 2001; Kokko and Sutherland, 2001; Kristan, 2003; Abrams et al., 2012; Fletcher et al., 2012; Hale et al., 2015). A vivid example of the lethality of traps is the extinction of an ecologically trapped population of butterfly following changes to land management which rapidly deteriorated the quality of oviposition sites (Singer and Parmesan, 2018). Yet, empirical evidence of the impact of traps on the viability of populations remains scarce (Robertson et al., 2013; Hale and Swearer, 2016), hindering our understanding of the urgency to intervene. And despite a solid theoretical framework and a growing range of examples, there is also limited information on how best to free populations from ecological traps (Robertson and Hutto, 2006; Robertson et al., 2013; Hale and Swearer, 2016).

A key finding in the simulation studies exploring the demographic consequences of ecological traps is the crucial importance of spatial factors – such as the proportion of trap habitat in the landscape – in determining the probability of population or metapopulation extinction (Battin, 2004; Fletcher et al., 2012; Hale et al., 2015). In the specific context of traps created by human harvesting, Abrams et al. (2012) accordingly argued that population extinction could occur when spatially limited hunting affected the focal population in the most productive areas of its range. From a conservation and management perspective, identifying the spatial distribution of factors causing ecological traps could pinpoint areas as prime targets for intervention. For instance, Sanchez-Mercado et al. (2014) combined spatially explicit models of human poaching and occurrence of Andean bears to predict the spatial distribution of potential traps at a broad spatial scale and suggest areas for management action. Empirical examples that clearly demonstrate the links between the distribution of spatial factors causing ecological traps and demography, however, are rare. A more spatially explicit and demographic approach relating animal use of space to population dynamics (Matthiopoulos et al., 2015; Doherty and Driscoll, 2018) could lead to insights into how best to intervene to mitigate the impact of ecological traps on vulnerable populations.

The objectives of this study were 1) to empirically evaluate the demographic consequences of an ecological trap and 2) to link use of space to survival and population viability to identify areas where management interventions would have the greatest impact on population persistence over the short term. Sigaud et al. (2017) have demonstrated that the free-ranging population of plains bison of Prince Albert National Park (PANP), Canada, is caught in an ecological trap caused by harvesting by humans in agricultural fields outside the protected area. However, because other sources of mortality such as wolf predation (Harvey and Fortin, 2013) and anthrax outbreaks also intervene (Shury et al., 2009), the impact of the trap on the viability of the population remains unclear. Agricultural fields were broadly identified as trap habitat by Sigaud et al. (2017), but the possibility that some fields might be more problematic to population persistence than others has yet to be explored. Finally, no information is available on where and how best to intervene to free the population from the ecological trap. Such information would be significant because the plains bison herd of PANP is one of the few wild populations of this threatened subspecies in the country (COSEWIC, 2013). We first used matrix population models parametrized with empirical data to evaluate the impact of the ecological trap on the population's viability. We then quantified the link between a key spatial attribute and population persistence to identify priority areas for intervention and provide a measurable target for management action.

## 2. Materials and methods

This section is organized as follows: we first detail the study

population and conservation context followed by a description of Global Positioning System (GPS) and habitat data. We then report how we obtained the empirical data on demography needed to parametrize the matrix model before describing it in detail. We end this section by describing the Cox proportional hazards model used to link habitat use to adult female mortality, and how we incorporated this relationship into the matrix model.

### 2.1. Study population and conservation context

Plains bison are large, gregarious herbivores characterized by relatively long lifespans (> 20 years in the wild), low fecundity and low intrinsic rates of population growth (Meagher, 1986). Females reach sexual maturity at 2 to 4 years of age, and usually give birth to a single calf between mid-April and May, every year or every other year (Meagher, 1986). As in other polygynous species in which only a few, large males breed with most females, the latter drive population dynamics in bison (Fuller et al., 2007). We thus focused our analyses solely on females, and classified them in three stages: calves (< 1 year old), juveniles (1 and 2 years old) and adults ( $\geq 3$  years old) (Merkle et al., 2015).

A free-ranging population of plains bison occupies the southwest corner of PANP (53°44' N, 106°39' W) and adjacent lands. The population was founded in 1969 by a group of 10 to 15 individuals from an original batch of about 50 released some 60 km north of PANP to serve as food to local Native Americans (COSEWIC, 2004). Bison use of agricultural fields outside PANP increased rapidly as abundance steadily declined from 500 in 2005 to just over 200 individuals in 2013 (Sigaud et al., 2017). Increased bison use of agricultural fields has led to greater damage to crops and infrastructure, and thus to dissatisfaction among some local landowners, a few of whom grant hunting permission on their lands. Only Native American hunters are legally entitled to hunt bison on these fields. The hunt only takes place when bison are out of the protected area, i.e. from July to the end of November. Most recorded harvest events took place from late August to November (see Section 2.6 below for a description of harvest data). Managers are under pressure to devise interventions to safeguard the population without detracting from its conservation value. Completely fencing the animals inside the park would mean the population is no longer free ranging, reducing its conservation value, while banning the harvest altogether would prevent indigenous cultural use of bison. Both are criteria used to assess the significance of individual populations to the overall conservation of bison in North America (Sanderson et al., 2008).

### 2.2. Global positioning system (GPS) and habitat data

From 2005 to 2016, we obtained location data from 48 adult females equipped with GPS radio-collars (4400M collar from Lotek Engineering Inc., Newmarket, ON, Canada, or TGW 4780H collar from Telonics Inc., Mesa, AZ, USA), 12 of which were harvested. We extracted locations from July to the end of November only, the period when bison venture into agricultural fields and are subject to human harvesting. Each individual was monitored from 1 to 8 years, with most tracked for 1 ( $N = 15$ ) or 2 years ( $N = 13$ ). The mean number of females monitored in a given year was 10 (range: 5 to 15). Locations were taken every 1 or 3 h.

Landcover types in the population's range were obtained from a classified SPOT5 10 × 10 m multispectral image dated from August 2008 (see full description in Dancose et al., 2011). Yearly fieldwork since 2008 has not revealed any major modifications to the configuration of the landscape in or outside PANP. Bison range from July to the end of November, as delineated by the 95% minimum convex polygon (MCP) built with all GPS location data from 2005 to 2016, covered 25,000 ha. Inside the protected area, bison range is composed of 83% of forest, 10% of meadows, 6% of water bodies and 1% of rivers and trails. Outside the protected area, bison range is mostly composed

of agricultural fields (56%). During the study period, the area of agricultural fields was composed of 20% of fields with hunting permission, 11% of fields without hunting permission, and 25% of fields not used by bison due to the presence of fences and other infrastructure blocking bison access. Forest patches accounted for 29% and meadows for 13% of the bison range outside PANP, whereas roads, rivers and water bodies accounted for the remaining 2%.

### 2.3. Photography data: tracking adult females through time

We used the approach developed by Merkle and Fortin (2014) to identify adult females in the population through time. The method relies on measuring phenotypic traits of bison horns (e.g. length and curvature) and face (e.g. distance between the eyes) from photographs. From the beginning of May to the end of August 2015 to 2017 and for 6 days a week, we visited meadows and agricultural fields regularly used by bison (as revealed by GPS data) and attempted to acquire high-quality photographs of the face of all adult individuals present in the group. We also took pictures opportunistically on trails and roads. A photography session could last anywhere from 10 min to 6 h, and only the research team took photos. We relied on GPS locations and VHF signals to find groups containing collared females, but we also regularly patrolled meadows and agricultural fields in search of groups with no collared females. We visited each meadow or agricultural field used by bison from July to November at least once on a weekly basis. Bison live in fusion-fission societies in which group size and composition changes through time, and accordingly dyads of GPS-collared females remain together for a median time of 21 h following a fusion event in summer (Fortin et al., 2009). By tracking the locations of 8 to 15 GPS-collared females each year and by regularly visiting all food patches used by bison over a four-month period, it is likely that we succeeded in photographing most adult females in the population each year at least once.

We photographed bison from a hidden position at 50 to 300 m away. We used an EOS Canon Rebel XS 10.1-megapixel camera with a fixed Canon EF 400-mm lens, and a 2× Canon extender (Canon Canada Inc., Mississauga, ON, Canada) mounted on a tripod. We also used the photograph set from 2011 to 2013 (Merkle and Fortin, 2014), which was obtained following methods similar to those described here. In total, 1306 photographs of adult female bison were available for identification. We took pictures of GPS-collared females with numbered ear tags (i.e. known individuals) to quantify and correct false-rejection and true-rejection rates, and we also quantified and corrected measurer bias (Merkle and Fortin, 2014; Cruickshank and Schmidt, 2017). A detailed account of these corrections is provided in Appendix A in Supplementary material.

### 2.4. Capture-mark-recapture (CMR): estimating abundance and survival probability of adult females

By using the dates when photographs were taken, the intra- and inter-year classifications (2011–2013 and 2015–2017) of unique adult females were used to create capture histories to estimate their annual abundance and survival probability. In the first case, for every year of analysis, the period spanning from 5 May to 26 August was divided into 8 capture occasions (i.e. the period in which each adult female was photographed at least once, or not at all) of 14 days each. In the second case, each year corresponded to a capture occasion. If more than one picture of a given female was available during each capture occasion, we only used the best photograph available during that occasion. CMR analyses were conducted using program MARK (White and Burnham, 1999).

Annual abundance of adult females was estimated using the Otis et al. (1978), full likelihood model for closed populations given that negligible emigration, immigration, births or deaths occurred during the 14-day capture periods. Previous research has demonstrated that CMR data obtained from photography yielded abundance estimates for

PANP bison that were consistent with those obtained from aerial counts (see Merkle et al., 2015, Appendix D, Table D4). Estimates of survival were calculated using a Cormack-Jolly-Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965) in which survival and capture probabilities were allowed to vary over time. Capture probability was held fixed within two periods to reflect methodological differences: in 2011–2013, two teams searched for bison and took pictures; in 2015–2017, only one team did so.

### 2.5. Stage ratios: estimating the abundance of female calves and juveniles

We followed Merkle and Fortin (2014) and used stage ratios to estimate the abundance of juveniles and calves. From 2015 to 2017, we counted the number of calves, juveniles and adults in bison groups observed in July and August (i.e. following the peak in births – see ratio data in Table B1 in Appendix B). For the 2011–2013 period, we used ratios published in Merkle et al. (2015, Table D4). We considered a sex ratio of 1 to divide ratios in half and account only for females (Fuller et al., 2007).

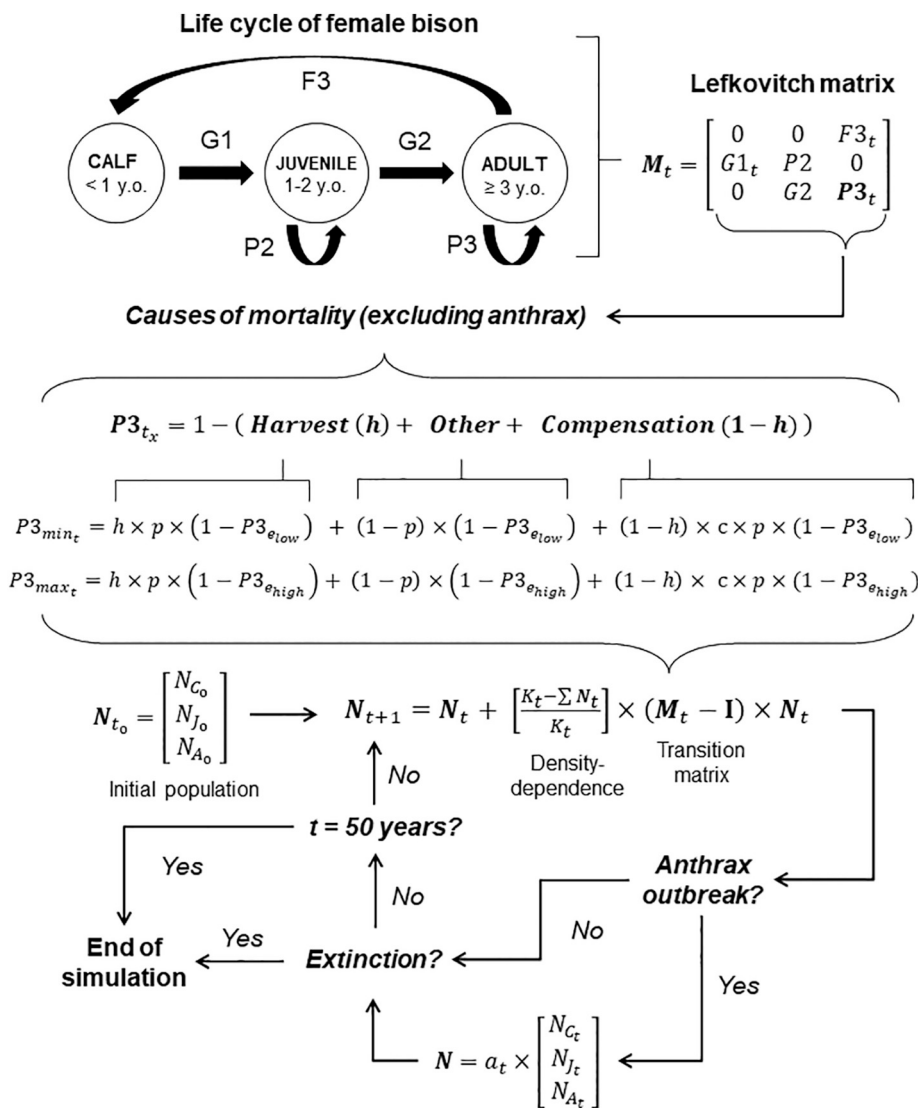
### 2.6. Harvest data: minimum estimate of the proportion of mortality due to harvest

Agricultural fields within the bison range were patrolled daily from July to November 2011 to 2016, and harvest events were recorded either from direct field observations or inferred from remains (i.e. presence of carcasses or gut piles). Some hunters also voluntarily provided information. The number, age and sex of the individuals harvested were recorded when possible. We observed a mean of 23 individuals harvested/year (range of 20 to 26), including the 12 females equipped with GPS collars. Despite the relatively intense monitoring effort, however, it is probable that some mortality events were not recorded.

We used the abundance ( $N$ ) and survival ( $\phi$ ) estimates obtained through CMR to estimate the number of adult females that died in year  $t$  [i.e.  $N_t \times (1 - \phi_{t \rightarrow t+1})$ ]. We then used the number of known females harvested/year to estimate the proportion of total mortality due to harvest. We assumed this proportion to be equal among stages because we had no clear evidence that hunters targeted a particular stage. The proportion of harvested individuals per stage (median and range of adults = 0.41, 0.13–0.71; juveniles = 0.21, 0.14–0.35; calves = 0.07, 0.00–0.17; unknown stage = 0.32, 0.04–0.48;  $N = 6$  years) was roughly equivalent to the proportions available in the population (median and range of adults = 0.65, 0.53–0.77; juveniles = 0.21, 0.11–0.29; calves = 0.14, 0.09–0.18;  $N = 6$  years – see also Fig. B1). We also had no evidence that hunters targeted a particular sex (median proportion and range that were female = 0.39, 0.13–0.46; male = 0.29, 0.17–0.55; unknown sex = 0.36, 0.04–0.70;  $N = 6$  years – see also Fig. B1).

### 2.7. Stochastic matrix population model: projecting current conditions into the future

We built a Lefkovich matrix population model (Caswell, 2001) incorporating simple density-dependence (Jensen, 1995), stochasticity, uncertainty and several sources of mortality (i.e. harvest, anthrax and other – see Fig. 1 for an overview of model configuration, scheduling and mathematical underpinnings). Assessments of the impact of human harvesting on populations have been criticized for failing to account for such complexity inherent to biological data (Weinbaum et al., 2013; Van Vliet et al., 2015). We determined an average carrying capacity of 250 female bison based on the 2005 peak of roughly 500 bison (Merkle et al., 2015). To account for environmental stochasticity and uncertainty, however, we allowed carrying capacity to vary between 200 and 350 females for every year of simulation ( $K_t$  in Fig. 1). The density dependent model of Jensen (1995) assumes linear, negative density



**Fig. 1.** Overview of the model used to evaluate the sustainability of the harvest driving an ecological trap for bison in lands adjoining Prince Albert national park, Canada. Subscript  $t$  indicates that values vary with time. Variable  $h$  determines the presence ( $= 1$ ) or absence ( $= 0$ ) of harvest. *Other* refers to wolf predation and additional causes of death (e.g. accidents, old age). The value of adult female survival ( $P3_t$ ) for each simulation was drawn randomly between  $P3_{min_t}$  and  $P3_{max_t}$ , the calculation of which is shown in the horizontal brackets.  $P3_{e_{low}}$  and  $P3_{e_{high}}$  are constants representing the lowest (0.71) and highest (0.87) values of adult female survival estimated empirically. Parameter  $p$  is the proportion of mortality due to harvest,  $c$  is the proportion of compensation, and  $a$  is the proportion of mortality due to anthrax. Other vital rates were also drawn from empirical intervals, with the exception of  $P2$  for which only one estimate was available.  $P2 = G2$ . Initial stage numbers were drawn randomly (see main text).  $N_t$  is the stage structure vector and  $I$  is the  $3 \times 3$  identity matrix.

**Table 1**

Estimates of abundance and associated 95% confidence intervals obtained through photographic capture-mark-recapture for female bison caught in an ecological trap in lands adjoining Prince Albert national park, Canada, from 2011 to 2013 and 2015 to 2017.

| Year | Adult           | Juvenile<br>(1–2 years old) | Yearling   | Two years<br>old | Calf       |
|------|-----------------|-----------------------------|------------|------------------|------------|
| 2011 | 93 (72–114)     | 10 (7–12)                   | –          | –                | 11 (8–14)  |
| 2012 | 84 (71–97)      | 19 (16–23)                  | –          | –                | 15 (12–18) |
| 2013 | 99 (91–107)     | 21 (19–24)                  | –          | –                | 13 (11–16) |
| 2015 | 66 (56–76)      | 20 (16–23)                  | –          | –                | 17 (14–20) |
| 2016 | 72 (65–78)      | 28 (24–33)                  | 16 (13–18) | 12 (11–15)       | 18 (15–20) |
| 2017 | 65 <sup>a</sup> | 21 (18–23)                  | 12 (11–13) | 9 (7–10)         | 7 (5–8)    |

<sup>a</sup> Results suggest all adult females were photographed at least once in 2017.

dependence so that vital rates are least impacted by density at lower densities but most reduced at higher densities (Morris and Doak, 2002). To assess the impact of this assumption on our results, we ran additional simulations with a fixed value for  $K$  varying from 250 to 1000 females by intervals of 150 (i.e. 250, 400, 550, 700, 850 and 1000). Uncertainty was also accounted for in the initial population ( $N_{t_0}$  in Fig. 1); numbers were drawn randomly from the corresponding 95% confidence interval obtained for 2016 (Table 1).

We simulated three scenarios to determine the impact of the

ecological trap on the viability of the population. Scenario 1 included all causes of mortality, Scenario 2 excluded anthrax, and Scenario 3 excluded harvest. We also determined how strong compensatory mortality would have to be, in the absence of harvest and given  $N_b$ , for the population to remain stable (i.e. mean population growth rate  $\bar{\lambda} = 1$ ). Compensatory mortality accounts for the possibility that some individuals harvested would have died anyway from non-hunting causes. For species with relatively low productivity and long generation time such as bison (Meagher, 1986), compensation by natural mortality in a scenario of exploitation is expected to be low (Lebreton, 2005; Peron, 2013). We defined a binary variable  $h$  to indicate the presence ( $= 1$ ) or absence ( $= 0$ ) of harvest mortality in each scenario (Fig. 1) and ran 1000 simulations comprising 50 years of simulation for any given set of parameters.

We used the minimum estimate of the proportion of females harvested per year (0.32 for 2011–2012, Table 2) as a fixed parameter determining the proportion of mortality due to harvest in every simulation ( $p$  in Fig. 1). Anthrax outbreaks, when present, were always modelled as fully additive, and their probability of occurrence was modelled stochastically. Based on the recurrence of outbreaks in Wood Buffalo National Park (WBNP) from 1963 to 2008 (Salb et al., 2014), we used a probability of 0.174 outbreak/year. The annual probability of anthrax outbreaks in PANP should not exceed this figure since only one outbreak has been recorded in the park so far (Shury et al., 2009). The



**Table 2**

Estimates of adult female survival with 95% confidence intervals and minimum estimates of the proportion of total mortality due to human harvest per year for adult female bison caught in an ecological trap in lands adjoining Prince Albert national park, Canada, from 2011 to 2017. Survival estimates were obtained through photographic capture-mark-recapture.

| Year      | Survival estimates and 95% CI | Estimate of total dead | Confirmed death due to harvest | Prop. due to harvest |
|-----------|-------------------------------|------------------------|--------------------------------|----------------------|
| 2011–2012 | 0.79 (0.65–0.88)              | 19                     | 6                              | 0.32                 |
| 2012–2013 | 0.83 (0.66–0.93)              | 14                     | 5                              | 0.36                 |
| 2013–2015 | 0.65 (0.56–0.72) <sup>a</sup> | 35 <sup>a</sup>        | 12 <sup>a</sup>                | 0.34                 |
| 2015–2016 | 0.71 (0.58–0.82)              | 18                     | 6                              | 0.33                 |
| 2016–2017 | 0.87 (0.69–0.95)              | 9                      | 6                              | 0.67                 |

<sup>a</sup> Over two years.

proportion of individuals killed by anthrax ( $a$  in Fig. 1) was drawn randomly from between 2 and 10%, according to the range observed in WBNP (Salb et al., 2014) and PANP (Shury et al., 2009).

We incorporated additional stochasticity in vital rates by randomly drawing values, for every year of simulation, from intervals obtained from empirical data using a uniform probability distribution (Fieberg and Ellner, 2001). Adult fecundity ( $F_{3t}$  in Fig. 1) thus varied from a minimum of 0.11 (7 female calves/65 adult females in 2017, Table 1) to a maximum of 0.26 (17 female calves/66 adult females in 2015, Table 1). The probability of calf-yearling transition ( $G_{1t}$  in Fig. 1) varied from a minimum of 0.69 (12 female yearlings in 2017/18 female calves in 2016, Table 1) to a maximum of 0.94 (16 female yearlings in 2016/17 female calves in 2015, Table 1). However, we used a fixed value for the probability of yearling-2-year-old transition ( $P_2$  in Fig. 1) because we only had one estimate for this vital rate (0.56, given 16 female yearlings in 2016/9 female 2-year-old juveniles in 2017, Table 1). Because we did not have abundance estimates for 3-year-old females, the probability of 2-year-old juveniles reaching adulthood ( $G_2$  in Fig. 1) was ascribed the same value as  $P_2$ . Finally, adult female survival ( $P_{3t}$  in Fig. 1) was also randomly drawn from an interval built using empirical values, but additionally accounting for the sources of mortality present in each scenario (see Fig. 1 for how this interval was calculated and Table 2 for empirical values of survival).

## 2.8. Cox proportional hazards model: linking adult female survival to the intensity of use of agricultural fields with hunting permission

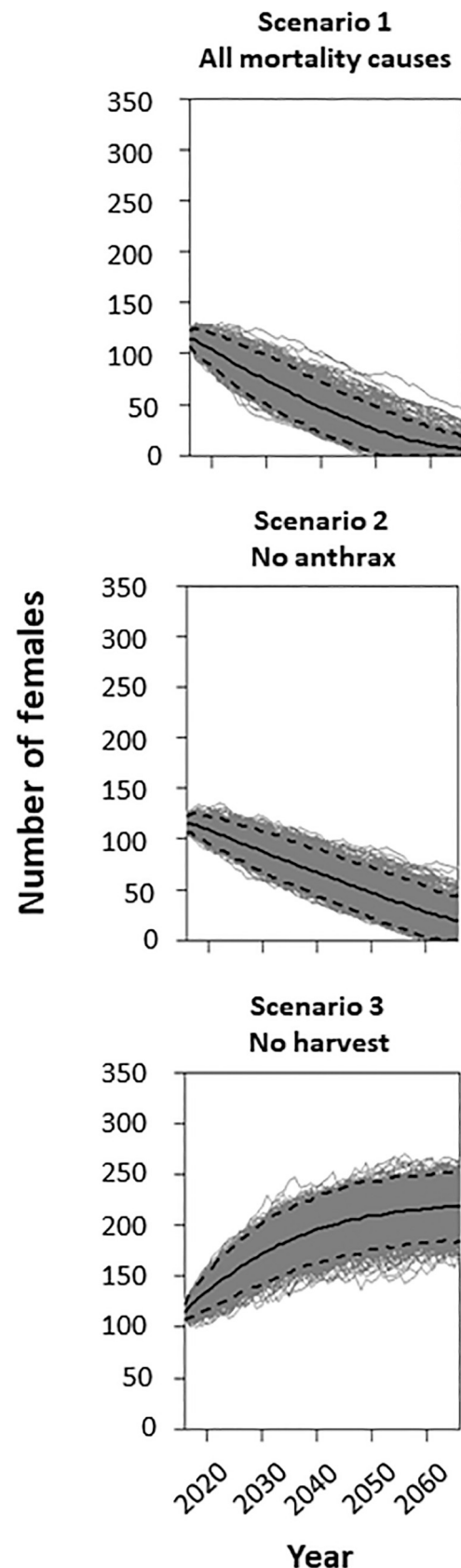
We built a Cox proportional hazards model using GPS data to link the percentage of time adult female bison spent on fields with hunting permission in a year ( $perm$ ) and their annual probability of survival. We used a recurrent time model (Fieberg and DelGiudice, 2009) from 1 January to 31 December with a daily time step, and accounted for within-individual correlation by estimating robust variances (as in DeCesare et al., 2014).

## 2.9. Spatially explicit population viability analysis: linking the intensity of use of fields with hunting permission to population persistence

We modified the stochastic matrix population model described above by relating adult female survival ( $P_{3t}$  in Fig. 1) to the percentage of time spent on fields with hunting permission ( $perm$ ) using the relationship obtained from the Cox proportional hazards model:

$$P_{3t_e | perm} = P_{30}(t_e) \exp(perm \times \beta_{perm})$$

where  $P_{3t_e | perm}$  is the survival rate at the end of the year,  $P_{30}(t_e)$  is the baseline cumulative survival probability to the last day of the year and  $\beta_{perm}$  is the coefficient obtained for covariable  $perm$  (the approach



(caption on next page)

**Fig. 2.** Stochastic projections of the abundance of female bison in Prince Albert national park and adjoining lands, Canada, for the next 50 years under three scenarios. Causes of mortality are harvest by humans, anthrax outbreaks (disease) and other (i.e. wolf predation, accidents and old age). Presence of harvest mortality indicates that the population is caught in an ecological trap (i.e. maladaptive habitat selection, see main text). Graphs show the 1000 simulations of each scenario (in grey) along with the mean (straight black line) and the associated 95% confidence interval (dashed black lines).

used here is similar to DeCesare et al., 2014). For each year of population projection, the value of  $P_{30}(t_e)$  was randomly drawn, using a uniform probability distribution, from the 95% confidence interval of the baseline cumulative survival probability estimated from the Cox model (i.e. 0.84–0.96). All analyses were performed using program R (R Core Team, 2015).

### 3. Results

Estimates of abundance for 2011 to 2013 and 2015 to 2017 showed a declining trend in the adult female component of the population (Table 1), while estimates of survival of adult females ranged from 0.71 to 0.87 (Table 2). Empirical estimates of the proportion of total mortality due to harvest varied from 0.32 to 0.67 (Table 2).

Projecting the current levels of mortality into the future, while accounting for stochasticity and the risk of new anthrax outbreaks (Scenario 1), resulted in a 66% probability of population extinction over the next 50 years (Fig. 2). Removing anthrax mortality altogether (Scenario 2) did not prevent population abundance from declining over the same period (Fig. 2). Removal of harvest mortality, however, led to population growth (Scenario 3, Fig. 2). In the absence of harvest and given current population abundance (i.e. about 100 to 120 females, Table 1), other causes of death would have to substitute for 55% and 71% of current harvest mortality to lead to a stable population (i.e.  $\bar{\lambda} = 1$ ) in the presence and absence of anthrax, respectively (see also Fig. C1 in Appendix C). Under typical conditions, the bison population in PANP should therefore increase in the absence of the harvest driving the ecological trap. Additional simulations showed that the proportion of total mortality due to harvest ( $p$ ) should not exceed 17% and 23% to prevent a decline in population numbers in the presence and absence of anthrax, respectively (see also Fig. C1). Increasing carrying capacity to up to 1000 females did not affect results, only the time it took for the population to plateau in Scenario 3 (Fig. 2).

When outside the park, 80% of the locations of collared females were on agricultural fields, and about 78% of individuals harvested were harvested on fields with hunting permission. The Cox proportional hazards model revealed that every 1% of additional time in the year bison spent on agricultural fields with hunting permission increased their hazard of being harvested by 9.2% ( $\beta = 0.088$ , robust se = 0.042,  $z = 2.127$  and  $p = 0.03$ ). Scaled Schoenfeld residuals did not covary with time ( $\chi^2 = 0.0009$ ,  $p = 0.98$ ), so the proportionality assumption of the Cox model was upheld. From 2011 to 2016, GPS-collared females spent 10% of their time on fields with hunting permission. Using this value as input in the spatially explicit model led to population extinction in 90% and 45% of 1000 simulations with and without anthrax outbreaks respectively (see also Fig. C2). Additional simulations showed that bison use of fields with hunting permission would have to drop to 3.0% and 5.5% in the presence and absence of anthrax respectively (i.e. a 70% and 45% decrease from the 2011–2016 figure respectively) to ensure population viability (i.e.  $\bar{\lambda} = 1$ , see also Fig. C2) over the next 50 years under current conditions. Just five fields – accounting for 235 ha or only 0.94% of the population's 25,000-ha home range from July to November (95% MCP), but representing the location of 70% of observed harvest mortality on fields ( $N = 124$  recorded deaths on fields out of 138 in total) – already account for > 70% of the intensity of bison use of fields with hunting permission (Fig. 3).

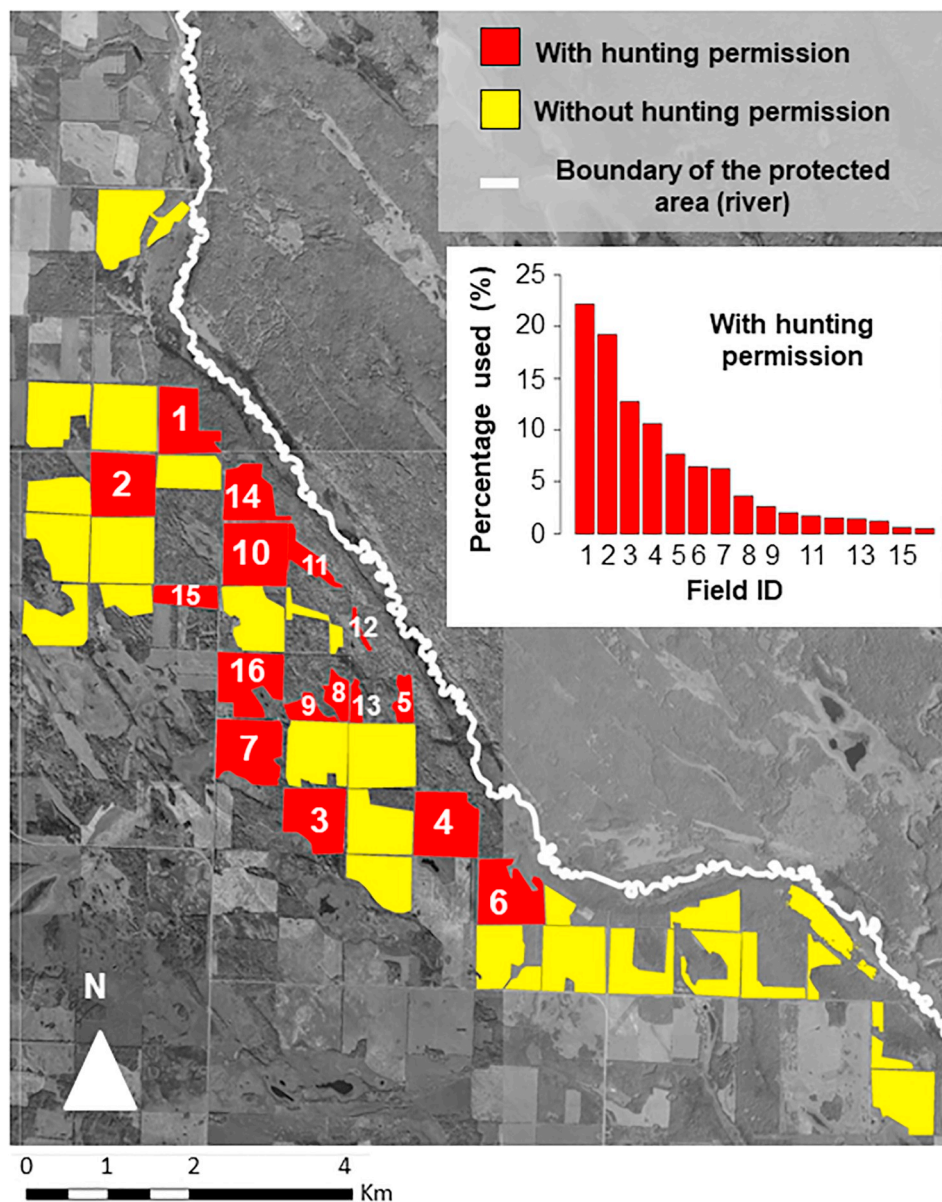
### 4. Discussion

In this study, we demonstrate that spatially explicit models linking fine-scale use of space, survival and population viability can contribute to better understand the demographic consequences of ecological traps (Robertson et al., 2013; Hale and Swearer, 2016) in an empirical setting. Our approach can also pinpoint localized areas for management interventions that would be most effective in mitigating the impact of traps on population persistence. We reveal how animal use of a very limited portion of a landscape can essentially drive the dynamics of a vulnerable population ranging over a much larger area. And by quantifying by how much the use of such areas should be reduced to ensure population viability, we demonstrate that linking animal use of space to demography can lead to clear, measurable targets for management and conservation.

Our study provides empirical evidence that ecological traps can push a population towards extinction. While recent field-based studies on vertebrates (e.g. Lamb et al., 2017; Santangeli et al., 2018) and experimental studies on invertebrates (e.g. Duchet et al., 2018; Faldyn et al., 2018) have shown the impact of ecological traps on vital rates, few have demonstrated that the trap actually threatens the long-term viability of animal populations (but see Sherley et al., 2017; Singer and Parmesan, 2018). Such an insight is required, however, to establish the degree of urgency in intervening to release populations from the trap and ensure their viability. Given an estimated probability of extinction of 66% over the next 50 years under current conditions, urgency is indeed warranted in the case of PANP bison.

Limitations of our study include absence or a relatively low number of estimates for vital rates, particularly for juvenile survival (G2 and P2 in Fig. 1). Moreover, the fact that we could not find any evidence of hunter preference for males or females, or for a particular stage, could be due to small sample size ( $N = 6$  years). Sigaud et al. (2017) have suggested that hunters preferentially target individuals that are  $\geq 2$  years old, while anecdotal evidence suggests that hunters prefer females over males as the former offer more tender meat. Yet, given that the harvest rate of PANP bison is certainly greater than the minimum value of 0.32 of total annual mortality (Table 2) and that population extinction over the next 50 years is already expected under this minimum rate (Fig. 2), such limitations are unlikely to change our conclusions. If anything, hunter preference for adult females should hasten population decline. Our study is thus one of the few reporting unsustainable harvesting in a population of conservation concern in North America. Even if anthrax outbreaks were as recurrent in PANP as they were in WBNP from 1963 to 2008 (Salb et al., 2014), their impact would be insufficient to drive a long-term population decline in PANP bison (Scenarios 2 and 3 in Fig. 2). Other sources of mortality, including wolf predation, would have to compensate for at least 55% of current harvest mortality to prevent population growth in the absence of harvest. For a species leaning more towards the K end of r-K selection spectrum such as bison (Meagher, 1986; Eberhardt, 2002), such a high level of compensation by natural mortality is unlikely (Lebreton, 2005; Peron, 2013).

Simulation studies have highlighted that once the proportion of trap habitat in the landscape exceeds a certain threshold – which will vary depending on the trap's severity and the quality of the habitat elsewhere in the landscape – population and metapopulation extinction becomes a deterministic outcome (Delibes et al., 2001; Donovan and Thompson, 2001; Kokko and Sutherland, 2001; Kristan, 2003; Abrams et al., 2012; Fletcher et al., 2012; Hale et al., 2015). Our results demonstrate that even a minute proportion of trap habitat might be sufficient to drive a population to extinction. Indeed, we circumscribed the ecological trap for PANP bison to < 1% of the population's range during the hunting period of July to November. Under current conditions, continued bison use of this area over just a few months a year is likely to result in the disappearance of the population over the next 50 years. Sanchez-Mercado et al. (2014) have used occurrence models to also quantify and



**Fig. 3.** Agricultural fields with and without hunting permission used by bison in lands adjoining the southwest corner of Prince Albert national Park, Canada, from July to November 2005–2016. The histogram shows the percentage of locations on fields with hunting permission obtained from 48 GPS-collared adult females monitored during the same period. Fields 1 to 5 alone accounted for 72% of locations on fields with hunting permission and were the site of 70% of all bison harvest events recorded on fields from 2011 to 2016.

map the proportion of trap habitat in the landscape. Here we go a step further by demonstrating that linking animal use of space to demography can provide quantified targets for management interventions aimed at ensuring population persistence. In our case, this target is a 70% drop in bison use of fields with hunting permission given current conditions and the possibility of further anthrax outbreaks.

Our results suggest that localized interventions preventing or discouraging PANP bison from accessing the five agricultural fields mostly responsible for population non-viability should be an effective short-term solution to guarantee population persistence. Use of electric fences on bison trails leading to some of these fields is currently under way, but experimental evidence suggests that bison eventually learn to circumvent fences to create new trails (Sigaud, 2018). Another option would be to fence the actual fields themselves (Hayward and Kerley, 2009), but at least some landowners seem reluctant to do so, possibly because they do not want to bear the costs on their own. These can indeed be substantial and recurrent (Hayward and Kerley, 2009) as

bison often destroy fences when determined to gain access to a given field. An alternative strategy could be to cultivate, on problematic fields, alternate crops that are not attractive to bison (e.g. Gross et al., 2016). For both fencing and alternate crops, financial compensation could be offered as incentives to landowners (e.g. Ranjan, 2017). However, this might prove insufficient as people's tolerance of wildlife is not governed by economics factors alone, but often also involves cultural and ideological considerations (Hill, 2018). In any case, an adaptive management approach would be required (Williams and Brown, 2016) because bison would redistribute themselves in space following any such intervention, which means that the problem might just be transferred to other fields. Still, localized interventions over the short term would clearly be less costly and aggressive than completely fencing bison inside the park or banning the hunt outright.

Over the long term, however, a community-based conservation strategy accommodating the expectations and needs of all stakeholders involved would undoubtedly be best (Kansky and Knight, 2014; Nyhus,



2016; Soliku and Schraml, 2018). Ranglack and du Toit (2016), for instance, have advocated a harvesting strategy for bison in the Henry Mountains of Utah as a means of generating revenue, and therefore local support, for bison conservation. Efforts to encourage PANP bison stakeholders to collaborate for bison conservation are underway and give cause for hope that the ecological trap in which these animals are caught will eventually be disarmed.

## 5. Conclusions

We provide an empirical example showing that ecological traps can drive populations to extinction even when trap habitat represents only a minute proportion of a population's range. We further demonstrate that a spatially explicit, demographic approach based on fine-scale animal use of space can pinpoint limited areas as preferential targets for management interventions to disarm the trap. This approach should also be valid in identifying solutions to mitigate other cases of human-wildlife conflict stemming from animal excursions out of protected areas. Adopting a spatial approach can help managers and conservationists identify where and when best to intervene over the short term and thus avoid costly and potentially ineffective interventions.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.05.001>.

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