

## LETTER

# Collective decision-making promotes fitness loss in a fusion-fission society

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### Abstract

While collective decision-making is recognised as a significant contributor to fitness in social species, the opposite outcome is also logically possible. We show that collective movement decisions guided by individual bison sharing faulty information about habitat quality promoted the use of ecological traps. The frequent, but short-lived, associations of bison with different spatial knowledge led to a population-wide shift from avoidance to selection of agricultural patches over 9 years in and around Prince Albert National Park, Canada. Bison were more likely to travel to an agricultural patch for the first time by following conspecifics already familiar with agricultural patches. Annual adult mortality increased by 12% due to hunting of bison on agricultural lands. Maladaptive social behaviour accordingly was a major force that contributed to a ~50% population decline in less than a decade. In human-altered landscapes, social learning by group-living species can lead to fitness losses, particularly in fusion-fission societies.

### Keywords

*Bison bison*, collective decisions, ecological trap, fusion-fission, habitat selection, population dynamics, Prince Albert National Park.

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## INTRODUCTION

Making the most rewarding choice under uncertainty is a fundamental aspect of decision theory (Kording 2007), and is central to a broad range of scientific fields. In recent years, ecologists have become increasingly interested in understanding the decision-making process of social animals (Conradt & Roper 2005; Couzin *et al.* 2005; Strandburg-Peshkin *et al.* 2015). Research on the adaptive value of collective decisions suggests that wider sharing of decision-making often results in a beneficial outcome (Conradt & Roper 2003; Franks *et al.* 2003). For example by pooling widely varying individual navigational bearings, group members can identify a single, accurate direction towards a collectively known spatial target [The Many Wrongs Principle (Simons 2004)]. Such accuracy should confer fitness gains, as long as the group identifies a beneficial target.

On the other hand, collective decision-making may be costly if naïve individuals are induced unwittingly to explore risky habitats, which is a real possibility in human-altered environments that differ from those under which the organisms evolved (Schlaepfer *et al.* 2002). In such cases, social transmission of environmental knowledge can lead to the attraction of individuals to an 'ecological trap', which appears to be of high quality but in reality exposes animals to heightened risk of mortality, resulting in a net reduction in fitness (Robertson & Hutto 2006). Social interactions in fusion-fission societies can rapidly spread knowledge of such traps through a population.

Ecological traps often occur where anthropogenic environmental change happens over a much shorter time span than natural change, uncoupling the cues that individuals use to assess habitat quality. The selection of anthropogenic edges by disturbance-dependant forest birds is a well-studied example (Weldon & Haddad 2005). While these edge sites often have physical characteristics suitable for nesting, birds that choose to nest in anthropogenic edge habitat experience high predation pressure from the relatively high concentration of nest predators, thereby decreasing fitness. Ecological traps can lead to the rapid decline or extinction of animal populations (Fletcher *et al.* 2012), depending on the proportion of the population exposed to the trap.

Transmission of information among population members of social species depends on the stability and cohesiveness of groups because spatiotemporal variation in grouping patterns influences the opportunity for group members to interact with one another (Aureli *et al.* 2008). In social species, information such as the location of an ecological trap can spread particularly fast among individuals. Collective movement decisions by individuals wrongly informed about habitat quality could then induce fitness loss. Although fusion-fission societies are widespread among group-living animals (Couzin & Laidre 2009), research on collective decisions has mainly focused on more cohesive animal societies (Sueur *et al.* 2011). Such a gap in knowledge leaves the interplay between social information, fusion-fission dynamics, and the transmission of costly behaviours an open question.

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Our objective was to identify the mechanisms that led to the collapse of a threatened population of free-ranging plains bison (*Bison bison bison*) that reside at the interface between a protected park and agricultural lands. We hypothesised that agricultural lands constitute an ecological trap for bison, and that social learning mediated by group dynamics played a major role in the spread of such maladaptative behaviour throughout the population. Bison groups are characterised by strong fusion-fission dynamics, with group sizes ranging up to 150 individuals, and fission events occurring with a median frequency of once every 21 h (Fortin *et al.* 2009). The bison range inside Prince Albert National Park (PANP), Canada, is composed mainly of forest punctuated by a mosaic of meadows where bison forage. Bison also venture onto agricultural lands that border the park (Fig. 1), mainly between July and October. Plains bison can be harvested only when they are outside the park boundary, creating a clear potential for significant differences in bison mortality risk between inside and outside PANP.

To examine our hypotheses we quantified the following relationships: (1) selection for the most profitable plants; (2) the factors influencing use of agricultural patches; (3) the fitness consequences of selecting agricultural lands and (4) the influence of group knowledge on selection for agricultural lands by naïve individuals. While to our knowledge there is only one empirical study addressing social learning in bison (Merkle *et al.* 2015b), several studies have demonstrated the ability of cattle, a similar large and gregarious herbivore, to engage in social learning (Ralphs *et al.* 1994; Bailey *et al.*

2000). To test the inference that social learning of the use of agricultural lands could explain the habitat use patterns and population dynamics observed in bison, we built a simple model based on the key components of the study. We simulated information transmission and bison population size over time for a representative range of model parameters, specifically including whether or not social learning could occur, and compared model predictions to observed population size. Our study depicts the interplay between collective decisions, guided by the social transmission of faulty behaviour, and fitness in free-ranging animals.

## MATERIALS AND METHODS

### Study area and bison data

The bison range is composed of forests (75%), meadows (4%), agricultural lands (7%), water bodies (6%) and other land cover types (8%, including shrubs and riparian areas). Other large mammals in the study area include elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), black bears (*Ursus americanus*) and grey wolves (*Canis lupus*).

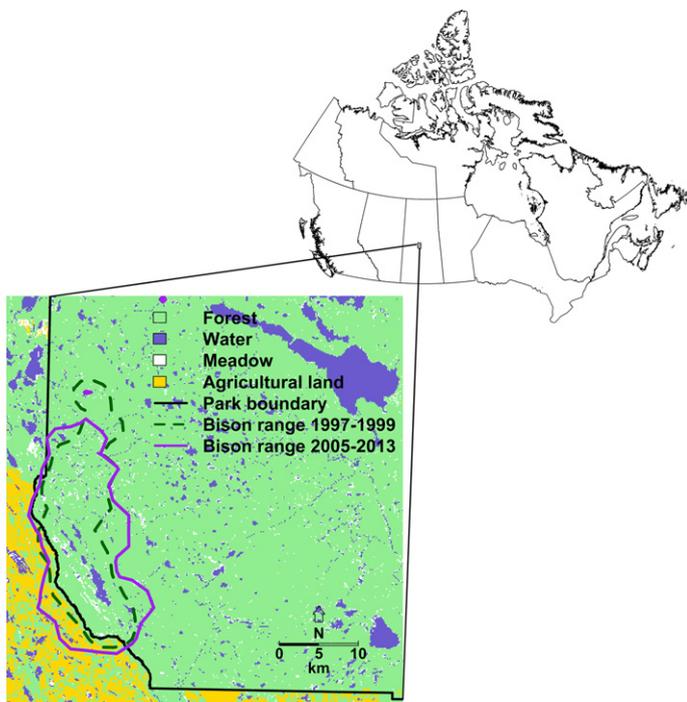
We equipped 49 adult female bison with either Global Positioning System (GPS) radio collars (4400M collar from Lotek Engineering Inc., New Market, Ontario, Canada) or Argos/GPS collars (TGW 4780H, Telonics Inc., Mesa, AZ, USA) between 1997–1999 and 2005–2013. GPS collars took locations every 3 h. Each bison was monitored for 21–574 days over 1–5 years. For our analyses, we used locations collected during summer and autumn, operationally defined as between 1 July and 31 October. This period encompassed 80% of bison locations collected on agricultural lands.

### Agricultural lands as an ecological trap

To evaluate whether agricultural lands were indeed an ecological trap, first we tested whether bison used the same foraging cues on agricultural lands as in natural environments. This test required surveying agricultural patches to estimate the profitability and relative use of available plants, and to evaluate how agricultural patch characteristics such as availability of profitable plants and distance to the PANP boundary influenced bison patch visits. Second, we assessed variation in selection of agricultural patches among years and individuals. Finally, we estimated the fitness consequences of this individual variation using two fitness surrogates: reproduction and survival.

### Testing selection for the most profitable plants and for agricultural lands

To evaluate plant selection, we calculated mean consumed and available biomass for each plant species every 2 weeks from early August to early November, in 26 agricultural patches (Appendix S1). We then performed compositional analysis (Aebischer *et al.* 1993), using individual agricultural patches as the sampling unit. We restricted our analysis to the six most common plant types [alfalfa (*Medicago sativa*), timothy (*Phleum pratense*), *Elymus* spp., *Poa* spp., *Trifolium*



**Figure 1** The study area in and around Prince Albert National Park, Saskatchewan (Canada). Dashed green line and solid purple line represent 90% contours of kernel distributions of all bison Global Positioning System (GPS) locations from 1997 to 1999 and 2005 to 2013 respectively. Between the 1990s and late 2000s plains bison expanded their range to include 236% more agricultural lands.

spp., *Bromus* spp.], which made up > 96% of biomass consumed on agricultural lands in early August to early November of 2011 and 2012.

To evaluate the profitability [i.e. ratio between digestible energy and handling time (Babin *et al.* 2011)] of the six different plant types, we first estimated the digestibility of dry matter (percentage of dry matter) of each plant type. We then calculated instantaneous intake of digestible energy (in kJ/min) for each plant species by multiplying the expected bison intake rate ( $I$ , g/min) by its digestible energy (DE; kJ/g; Fortin *et al.* 2002; Appendix S2).

To evaluate how the availability of profitable plants influences the use of agricultural lands by bison, we characterised (during August–October) 19 of the most commonly used agricultural patches in 2011, and 17 of the most commonly used patches in 2012. Agricultural patches were defined as homogeneous agricultural units with a single type of crop (or pasture) and often delineated by a fence or a tree line (Appendix S3). For each patch, we estimated the natural logarithm of its area (LogArea), the Euclidian distance between patch edge and the park boundary, and its mean normalised difference vegetation index (NDVI) value, obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS-TERRA) data set (250 m, 16 day resolution). NDVI closely predicted mean green biomass ( $G$ , in g/m<sup>2</sup>) in agricultural patches:  $G = 11.84 + 1.23 \times \text{NDVI}$  ( $r^2 = 0.70$ ,  $n = 60$ ,  $P < 0.001$ ; Appendix S1 and S3). We classified patches important for bison into four different categories depending on the dominant vegetation type determined by visual estimation: cereal grain (wheat (*Triticum* spp.), barley (*Hordeum vulgare*), oats (*Avena sativa*) or a mixture of these species), forage pasture dominated (i.e. representing more than 50% of the available biomass) by alfalfa, forage pasture dominated by timothy and mixed forage pasture. To identify variables related to the chance of a bison using an agricultural patch at a given time, we used a Cox proportional hazards regression model with a counting process formulation (Appendix S3). Cereal grain was identified as the reference category in the analysis and all continuous variables were standardised.

To assess changes in the selection of agricultural lands by bison from 2005 to 2013 during July to October, we used Resource Selection Functions (RSFs) in which habitat characteristics at observed GPS points (scored 1) were compared to random locations (scored 0) that defined habitat availability (Fortin *et al.* 2009). We defined availability as areas that were accessible to bison between 2005 and 2013 (Appendix S3). Observed and random locations were characterised by dummy variables representing land cover types, which were identified based on Landsat Enhanced Thematic Mapper (ETM+) satellite images taken in 2001 with a 28.5 m resolution (Fortin *et al.* 2009). Land cover types included agriculture, forest, meadow, road and other (including water, shrub and riparian area). Forest was the reference category. We used mixed-effects logistic regression to parameterise the RSF, with ‘individual’ and ‘year’ as random intercepts, representing 89 unique individual-year combinations. To evaluate variation in selection among individuals and years, we specified random slopes for meadow and agricultural lands. The robustness of the model was assessed using  $k$ -folds cross validation (Boyce *et al.* 2002).

#### Assessing fitness consequences of selecting agricultural lands

To investigate potential fitness benefits of selecting agricultural lands, we tested whether the strength of selection for agricultural lands could explain observed variation in pregnancy rates of bison. We determined late-term pregnancy (Feb–March) status of 19 adult females captured between 2006 and 2014 using rectal palpation. We fit a binomial generalised linear model to the data, with the individual-specific agricultural land selection coefficient derived from RSFs in the late summer and autumn (July–October) prior to capture as the predictor variable.

To evaluate potential fitness costs of foraging on agricultural lands, we monitored bison mortality due to hunting from August to early November in 2011, 2012 and 2013. We recorded the occurrence of harvested bison through direct observation of hunting events and carcasses or remains found on agricultural lands consistent with human harvesting (i.e. gut piles or carcasses with signs of butchering). On an opportunistic basis, we also recorded bison mortality events in PANP from 2011 to 2013. When carcasses or remains were recovered, we identified sex and age classes (< 2 years old;  $\geq 2$  years old) based on horn shape and body size, whenever possible. To allow comparisons between mortality due to harvest and other natural processes, we also computed the expected number of adult bison mortalities based on yearly estimates of the number of adult bison in the population (Merkle *et al.* 2015a).

#### Social learning promotes selection of an ecological trap

We built a patch selection model (Merkle *et al.* 2014) to test whether or not social learning promotes the selection of an ecological trap (Appendix S3). We considered two types of patches: meadows (> 0.04 ha) within PANP and agricultural fields delineated from a SPOT5 multispectral image (Dancose *et al.* 2011). For each observed patch-to-patch movement, we selected 20 potential target patches that the animal could have visited after departing the source patch based on a probability proportional to the resource-independent movement kernel. Given our interest in understanding patch selection with respect to agricultural lands, we only used patch-to-patch movements where at least one agricultural patch was present in the set of target patches.

For each target patch (observed and potential), we calculated the log of the area (LogArea), and the Euclidian edge-to-edge distance between the source and target patches. We then identified whether or not target patches that were classified as agricultural fields had been previously visited by the focal animal in the previous 1–2 years of monitoring (hence the first year of monitoring for every individual was used to quantify past experience and removed prior to parameterisation). Thus, target patches were classified as meadows (the reference category), or known or unknown agricultural fields. For each patch-to-patch movement, we also identified whether or not other simultaneously collared individuals were within the same group as the focal animal (Merkle *et al.* 2015b). Then, we calculated the presence of informed individuals among the focal individual’s fellow group members (coded as 1 if at least one group member already visited the target patch and 0

otherwise). Our inference was based on 2687 patch-to-patch movements by 22 individual female bison representing 35 unique individual-year combinations 2006–2013. We parametrised the patch selection model using conditional logistic regression. We calculated robust SE and 95% confidence intervals of parameters using generalised estimating equations (GEE) (Craiu *et al.* 2008). All strata for a given individual within a given year were assigned a unique cluster (i.e. 35 clusters) in the GEE analysis. The robustness of the model was assessed using  $k$ -folds cross validation (Fortin *et al.* 2009).

#### Model of information flow, spatial use patterns and population dynamics

To test the hypothesis that social learning of the use of agricultural lands could explain the habitat use patterns and population dynamics observed, we constructed a simple model based on the key components of the study (Appendix S4). The model shares similarities with Susceptible-Infected-Recovered models (Kermack & McKendrick 1927) of disease transmission and demographic consequences. Here, a naïve population of animals of density  $A$  is exposed to a population of informed individuals of density  $B$  within PANP that have already experienced habitats outside PANP. At any given time, a subpopulation of emigrants of density  $C$  is outside the park, where they experience heightened mortality due to harvest at a rate  $h$ . The total population  $N$  includes all the behavioural morphs. The equations for this set of behavioural transitions combined with demography are as follows:

$$\frac{d}{dt}A(t) = r[A(t) + B(t) + C(t)] \left(1 - \frac{A(t) + B(t) + C(t)}{K}\right) - sA(t) - fgA(t)B(t) \quad (1)$$

$$\frac{d}{dt}B(t) = eC(t) - gB(t) \quad (2)$$

$$\frac{d}{dt}C(t) = sA(t) + gB(t) + fgA(t)B(t) - eC(t) - hC(t) \quad (3)$$

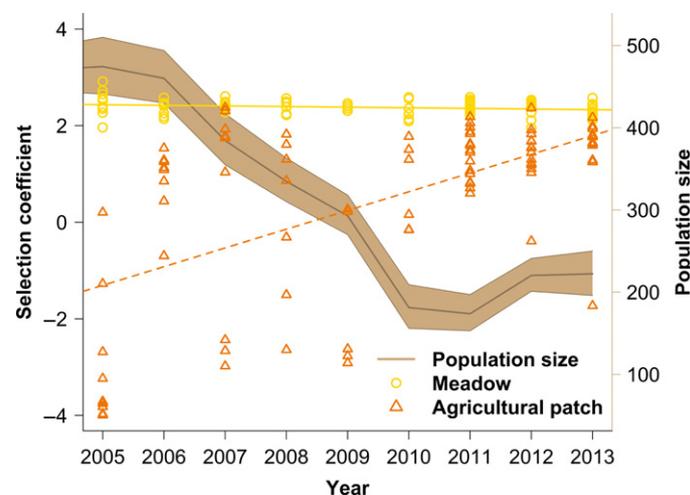
$$N(t) = A(t) + B(t) + C(t) \quad (4)$$

A small proportion ( $s$ ) of naïve individuals are expected to wander out of PANP on their own volition, simply as a result of exploratory movement behaviour (see eqn 1) resulting in asocial acquisition of the behaviour. Informed individuals leave the park at a rate,  $g$ . A proportion ( $f$ ) of the naïve individuals that encounter informed individuals leaving on forays outside of PANP are expected to follow them, and become emigrants through a social learning mechanism. All emigrants are exposed to harvest at rate ( $h$ ). Informed individuals transfer out of the park at a rate,  $g$ , while emigrants transfer back into the park at rate ( $e$ ). All behavioural morphs contribute to logistic population growth with a maximum per capita rate  $r = 0.20$  and carrying capacity  $K = 1600$ . Parameter  $r$  takes into account the exponential rates of natural mortality and recruitment (Fryxell *et al.* 2014). At the start of our simulations, we assumed that the population comprised only of uninformed individuals. We developed two sets of simulations to examine whether social learning is necessary to recover the observed population

trajectory and use of agricultural lands. We simulated population trajectories over 16 years for social and asocial learning via the parameter  $f$ , based on combinations of varying values of parameters  $h$ ,  $g$  and  $e$  (see Appendix S4 for details of the model). We used the residual sum of squares approach to assess each simulation's goodness of fit to data. All analyses were conducted using R (R 3.0.2; R Core Team 2013).

## RESULTS

When free-ranging bison left PANP and ventured onto agricultural lands (mainly during late summer and early autumn), they selected agricultural patches containing alfalfa and timothy, and selectively consumed these two plant species (Table S1 and S2; Fig. S1). The ratio between digestible energy and handling time made alfalfa and timothy the most profitable plant species available on both agricultural lands and meadows in the park during late summer and autumn (Table S3). Few bison used agricultural lands prior to 2006. Relative to their selection of forest, bison shifted from an overall avoidance of agricultural patches to selecting them over 9 years (2005–2013) (least-square regression, individual selection coefficient vs. year:  $F_{1,87} = 44.1$ ,  $r^2 = 0.34$ ,  $P < 0.0001$ ), with both the strength of this selection and the number of individuals selecting agricultural patches increasing over time (Fig. 2 and Table S4). This change in selection occurred even though vegetation quality and availability did not change in natural meadows among years (Merkle *et al.* 2015a) and bison continued to strongly select natural meadows over other land cover types (Fig. 2).



**Figure 2** Bison selection for meadows and agricultural patches and population size. Selection coefficients for meadows and agricultural patches by female plains bison in and around Prince Albert National Park, Saskatchewan (Canada) from July to October 2005–2013 (Table S4). Estimates derived from a mixed-effects Resource Selection Function (RSF, see Appendix S3). A positive coefficient indicates selection for a given land cover type with respect to forest, the reference cover type. Avoidance of agricultural patches prior to 2006 shifted to selection and increased thereafter (dashed orange line). Radio-collared bison ( $n = 40$ ) selected meadows (continuous yellow line) consistently across all years. Population size (brown line, with 95% CI) declined from 2005 to 2010, then remained relatively stable (Merkle *et al.* 2015a).

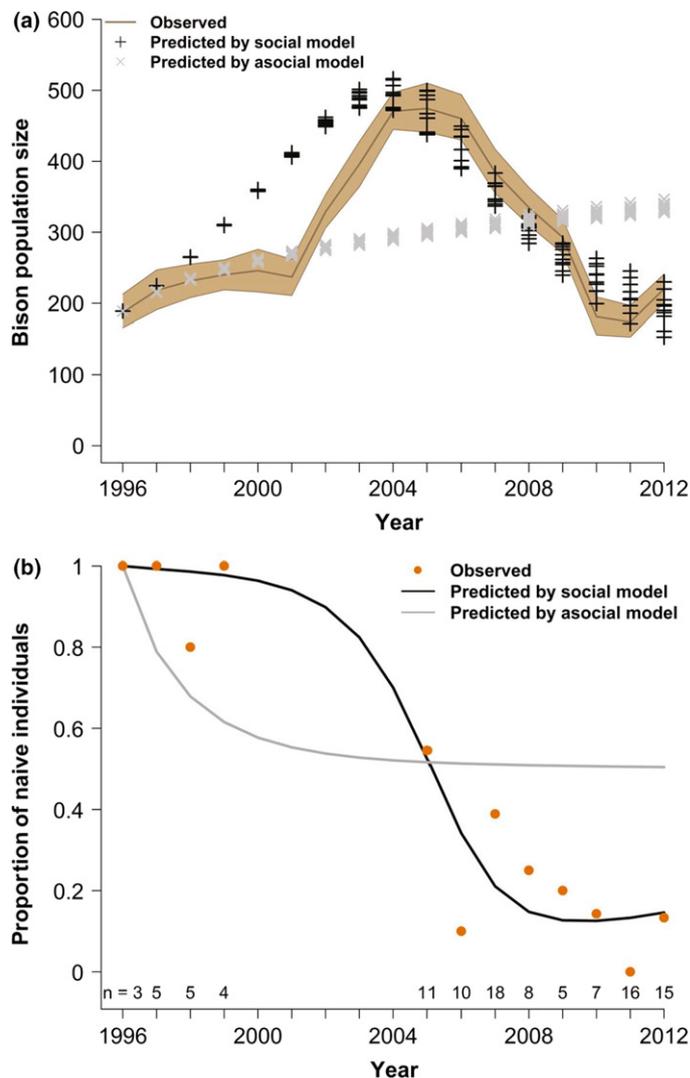
Despite strong variation in the gestation rate of bison among years (mean 0.66 with 95% CI = 0.55–0.76), selection of agricultural patches did not affect the probability of gestation ( $n = 19$  female bison,  $P = 0.77$ ). From 2011 to 2013, at least 61 bison were harvested outside PANP (mean of 21 bison per year), and we identified 20 bison (mean of 6.7 bison per year) that died of natural causes within PANP (note that our detection probability was likely lower inside than outside PANP). Based on a mean adult survival rate from the literature (92% based on Fuller *et al.* 2007), we estimated that 41 bison (mean per year 13.7) should have died of natural causes within PANP from 2011 to 2013. Furthermore, based on our sample of radio-collared animals ( $n = 61$ ), eight likely died from wolf predation and seven died from hunting. We do, however, suspect that hunters generally avoid harvesting collared bison. Of the 28 carcasses we recovered and sampled from bison harvested outside the park, 80% were  $\geq 2$  years old. Based on the age distribution of the population during the same period (Merkle *et al.* 2015a), the harvest represented 12% ( $\pm 2\%$ ) of the  $> 2$  year old age category each year. We note that these harvest numbers should be considered an underestimate because they were based mainly on the observations of bison remains. Hunters were not obliged to report their harvest and the hunt was unregulated.

Bison selected larger and closer target patches than available during patch-to-patch movements. Yet, when a collared bison was in a group that had at least one individual familiar with an agricultural patch, it was more likely to use the agricultural patch for the first time during its 12–63 month monitoring period (Table S5).

Our simulations of information flow and population dynamics showed that models including the social learning parameter ( $f > 0$ ) overall performed better at predicting observed population dynamics of bison than setting  $f = 0$  (i.e. asocial learning only) (Fig. 3). The asocial learning model, however, still accurately predicted the population trends during the first 6 years. In the top ranking models with social learning,  $f$  varied from 0.05 to 0.85 (Table S6). In accordance with observed trends in the use of agricultural lands, the best fitting model with social learning predicted that *c.* 80% of the population remained naïve to the use agricultural lands before 2005. After 2005, however, the ratio of naïve to experienced individuals shifted rapidly resulting in only 20% of the population being naïve at the end of the simulation (Fig. 3b). According to the best model without social learning, the naïve segment of the population stayed rather stable, at *c.* 60%, over time (Fig. 3b). In accordance with observed population trends, the best simulation predicted a population size increase over the first 8 years, peaking in 2004 with 507 individuals, before declining to 161 individuals by 2012 (Fig. 3a).

## DISCUSSION

One of the incentives for group formation is the ability to pool information and make more informed decisions when faced with environmental uncertainty. Collective decisions influenced by social learning should allow group-living organisms to reliably achieve collective wisdom through decision accuracy across diverse contexts. We found, however, that



**Figure 3** Temporal dynamics of knowledge acquisition about an ecological trap and simultaneous changes in population size. (a) Predicted population size (eqn 4) over time based on the 10 best fitting models with ( $f > 0$ ) and without ( $f = 0$ ) the social learning component, together with the observed bison population dynamics in and around Prince Albert National Park (PANP), Saskatchewan (Canada). (b) Percentage of naïve individuals in the population,  $A(t)/N(t)$ , as predicted from the best fitting collective behavioural model, see eqns 1–4, with ( $f > 0$ ) and without ( $f = 0$ ) the social learning component, and from observed radio-collared bison (sample size of bison indicated).

collective movement decisions misguided by an incorrect assessment of habitat quality can incur fitness loss in group living species.

### Agricultural lands as an ecological trap

Bison used similar cues, based on the profitability of forage plants, to assess high-quality foraging areas in agricultural patches and natural meadows (Fig. 2 and Table S4). As observed in natural environments (Babin *et al.* 2011), the abundance and distribution of highly profitable plants was a strong driver of bison behaviour. Energy gains are a main driver of habitat choice in many species. Since the 1950s, the

intensification of agriculture offers new feeding opportunities for several species. For instance, arctic-nesting geese (*Anser albifrons flavostris* and *Anser brachyrhynchus*) have shifted their range to exploit highly profitable forage provided by agricultural lands. During the last 50 years, this has resulted in an increase in goose population size through enhanced reproductive success (Fox *et al.* 2005). To guide their choice of habitat, organisms often use indirect cues that, over evolutionary time, reliably correlate with survival and reproductive success. However, if an environment changes suddenly, the normal cues might no longer correlate with the expected outcome (Schlaepfer *et al.* 2002).

We considered pregnancy rate and adult survival as surrogate measures of the fitness consequences of foraging on agricultural lands. In many ungulates, the availability and quality of forage in late summer and early autumn is critical to reproductive success. For example female mule deer (*Odocoileus hemionus*) with a lower intake rate of digestible energy during summer and autumn have a lower probability of conceiving and producing twins (Tollefson *et al.* 2010). Our failure to detect a reproductive benefit could be because there is considerable inter-annual variation in pregnancy and the small sample size of female bison tested for pregnancy during the study ( $n = 19$ ) made it difficult to detect an effect. That being said, the relatively short period of time bison used agricultural lands, even by experienced bison (mean  $58 \pm 4$  days/year, from 2011 to 2013), could also be inadequate to result in energy accumulation of sufficient magnitude to result in an overall reproductive benefit. Moreover, forage quality inside PANP might be sufficient to maintain a high reproductive rate. Indeed, the highest annual growth rate (0.39) was observed in 2002 (Merkle *et al.* 2015a), before bison started making extensive use of agricultural lands. Overall, we did not detect a reproductive benefit of foraging on agricultural lands.

In large herbivores, adult survival rate has low temporal variability but high elasticity (i.e. high proportional effect) and, therefore, has a stronger impact on population growth than any other vital rate (Gaillard *et al.* 2000). Accordingly, adult survival is a strong fitness correlate in large herbivores. For bison, adult survival is relatively stable despite fluctuations in forage availability (Vanvuren & Bray 1986), but can vary strongly depending on human-induced mortality (Plumb *et al.* 2009). From 2011 to 2013, we observed approximately three times as many bison to be killed by hunters on agricultural land than were observed to die of natural causes inside the park. Even though we were less likely to observe natural deaths inside the park, based on reported adult survival rates in the literature (Vanvuren & Bray 1986; Fuller *et al.* 2007), many more adult bison died outside the park due to human harvest than would have been expected to die of natural causes. These figures suggest a steep increase in the mortality rate of adults over natural mortality inside the park, a fitness cost that stems directly from anthropogenic risk associated with use of agricultural lands outside of the park.

There are several reasons that mortality from bison hunting should be at least partially additive to natural mortality. First, long-term monitoring of other bison populations demonstrates that annual adult survival is typically high, even in populations with a full suite of natural predators

(range 92–96%) (Vanvuren & Bray 1986; Fuller *et al.* 2007). Compared to short-lived species, long-lived taxa are predicted to have a lower ability to cope with anthropogenic mortality because their low and relatively constant natural mortality rate cannot compensate for an additional source of mortality (Gauthier *et al.* 2001). Second, hunting is unlikely to replicate natural predation in bison, as hunters select individuals  $\geq 2$  years old that have high reproductive value, whereas predators preferentially kill calves or individuals in poor condition with lower reproductive values. For example in Yellowstone National Park 60% of bison killed by wolves are  $< 2$  years old (Smith *et al.* 2000). In fact, there is little empirical evidence in medium and large-sized mammals that adult mortality from harvest can be fully compensatory (Bender *et al.* 2004; Sand *et al.* 2012). In summary, while agricultural lands provide higher quality resources than natural meadows available inside PANP, they come with a higher mortality risk and no detectable increase in reproduction. Indeed, the sharp decline in bison population size after 2005 implies that the costs of using agricultural patches outweighs the benefits.

#### Social learning promotes selection of an ecological trap

Our results showed that the observed population-wide shift from avoidance to selection of agricultural lands, and subsequent decrease in population size can be explained by collective movement decisions of bison groups. Group formation and the transfer of information among group members play an important role in the space use dynamics of gregarious species (Couzin *et al.* 2005). Group members must make coordinated collective decisions that maintain group cohesion and minimise reward uncertainty (Krause & Ruxton 2002). In fusion-fission societies, such as in bison, group stability is low and individuals are constantly associated with other animals possessing different spatial knowledge. Furthermore, bison are known to selectively return to patches that are both familiar and profitable (Merkle *et al.* 2014). Because agricultural patches are highly profitable, after visitation by a naïve individual, they likely become part of the individual's home-range (Table S3 and Fig. S1). Through collective decision-making, every new individual that learns about the profitable food on agricultural lands increases the probability that naïve individuals also visit agricultural lands for the first time.

Social learning is commonly assumed to be profitable, however, the use of socially acquired information can lead to informational cascades resulting in sub-optimal behaviour (Giraldeau *et al.* 2002). There are circumstances – e.g. when environmental conditions change suddenly – under which socially learned information is no longer relevant (Laland & Williams 1998). For instance free-ranging bottlenose dolphins (*Tursiops aduncus*) learn from each other how to obtain food from fisherman, which results in higher risk of boat strikes and entanglement (Donaldson *et al.* 2012). These results are consistent with our findings that social learning provides a mechanism for the rapid spread of costly behaviours through a population, and promotes the use of an ecological trap.

Empirical data directly supporting the presence of social learning are difficult to collect on free-ranging animals as it requires intensive field work and long-term monitoring (e. g. Allen *et al.* 2013; Hobaiter *et al.* 2014). The following hypotheses could provide alternative explanation for the population-wide shift from avoidance to selection of agricultural lands by bison: increase in foraging quality or availability on agricultural lands; increase in wolf predation inside the park; density dependence and asocial learning. However, there is little support for any of these hypotheses. Surveys conducted with 10 farmers regarding their farming practices (e.g. crop types and farming practices) between 2005 and 2010 together with our vegetation surveys conducted in 2010–2013 revealed no major changes in agricultural vegetation composition consistent with a major behavioural shift in bison habitat preferences (Appendix S1). Furthermore, we have been monitoring wolves in the park since 2007 via GPS collars, and there has been no shift in the centroid of the wolf pack territories closer to the bison range in the park over time ( $F_{1,8} = 0.48$ ,  $P = 0.5$ ,  $R^2 = 0.06$ ).

Finally, individuals can acquire new traits or behaviours through trial and error or direct interactions with the environment. Yet, our simulation results provide no evidence for a pure asocial learning mechanism to explain the population-wide shift from avoidance to selection of agricultural lands over time (Fig. 3a). During the period of population increase from 1996 to 2005, population range size increased involving the addition of new foraging patches (Merkle *et al.* 2015a). Bison density was high when bison began using agricultural lands, and could have possibly triggered the initial movement outside PANP. This behavioural mechanism could explain why the asocial model accurately predicted the population changes within the first few years. But density dependence does not appear to be a reason for the rapid behavioural shift, because as the use of agricultural lands increased, density decreased rapidly (Fig. 2). Alternatively, predictions from the SIR model support our conclusion that rapid transfer of patch selection behaviour from bison with experience travelling outside the park to naïve individuals within the park could readily lead to shifts in both habitat selection and population declines consistent with those of the PANP population (Fig. 3). Whereas this simple model does not take into account additional sources of mortality thought to occur in this population, such as anthrax, our model shows the observed population dynamics and habitat use could emerge simply through increased exposure to an ecological trap via social learning of maladaptive habitat selection behaviour.

Overall, we have demonstrated that group fusion-fission dynamics facilitated the acquisition of information about forage quality on agricultural lands, resulting in the propagation of this costly behaviour across an entire bison population in less than a decade. Social learning, particularly in fusion-fission societies, can therefore be a critical, but largely overlooked, factor in understanding the ecological consequences of ecological traps. More generally, our results suggest that when the environment has changed such that environmental cues no longer reflect reliable determinants of fitness, collective information processing may actually be detrimental to fitness.

## STATEMENT OF AUTHORSHIP

M.S. designed the research, collected field data, performed laboratory and statistical analyses. D.F. conceived the original idea. J.A.M. developed the patch selection model. J.M.F. and A.B. built the population model. All authors contributed to the study design and all authors discussed the results and commented on the manuscript.

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