

LETTER

To follow or not? How animals in fusion–fission societies handle conflicting information during group decision-making

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Abstract

When group members possess differing information about the environment, they may disagree on the best movement decision. Such conflicts result in group break-ups, and are therefore a fundamental driver of fusion–fission group dynamics. Yet, a paucity of empirical work hampers our understanding of how adaptive evolution has shaped plasticity in collective behaviours that promote and maintain fusion–fission dynamics. Using movement data from GPS-collared bison, we found that individuals constantly associated with other animals possessing different spatial knowledge, and both personal and conspecific information influenced an individual's patch choice decisions. During conflict situations, bison used group familiarity coupled with their knowledge of local foraging options and recently sampled resource quality when deciding to follow or leave a group – a tactic that led to energy-rewarding movements. Natural selection has shaped collective behaviours for coping with social conflicts and resource heterogeneity, which maintain fusion–fission dynamics and play an essential role in animal distribution.

Keywords

Animal distribution, *Bison bison*, collective decision-making, fusion–fission society, group dynamics, habitat selection, Prince Albert National Park, site fidelity, spatial memory, step selection function.

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INTRODUCTION

The evolutionary context underpinning movement decisions made by group-living animals is central to understanding socioecology and animal distribution patterns (Couzin & Krause 2003). To reap the fitness benefits of group living, group members must make coordinated collective decisions that maintain group cohesion and minimise reward uncertainty (Krause & Ruxton 2002). During collective decision-making, decisions are largely based on personal information possessed by individuals in frontal positions (Miller *et al.* 2013), with the behaviour of subsequent group members often driven by copying and quorum-like rules (Sumpter *et al.* 2008; Ward *et al.* 2008). These processes are the baseline for the reinforcement of accurate decisions as group size increases (Sumpter *et al.* 2008). Such findings, however, presume that knowledge is rather similar (i.e. each individual knows only one of a few possible options), and that groups only benefit through relatively stable cohesiveness (Sueur *et al.* 2011).

In fusion–fission societies where group stability is low, these presumptions will not always be met. The informational state of individuals in fusion–fission societies can vary widely due to dissimilar past experiences (Aureli *et al.* 2008; Sueur *et al.* 2011). Such disparate information will result in conflicts during group decision-making, leading to options for group members. First, leadership behaviour including personal (e.g. dominant individuals lead group decisions) or distributed (i.e. group decisions based on the option favoured by the majority) leadership can be implemented (Conradt & Roper 2005; Petit & Bon 2010). For example, in the case of conflicting travel directions, the type of group decision (e.g. take an average

direction favoured by all or choose among the preferences of some) is based on the degree that informed individuals disagree (Couzin *et al.* 2005; Dyer *et al.* 2008). Second, groups can temporarily break-up because group cohesion is not a strict rule (Kerth *et al.* 2006; Sueur *et al.* 2011). For instance, individual Bechstein's bats (*Myotis bechsteinii*) will temporarily leave their groups to avoid majority decisions about the choice of roosting sites that are not in their favour (Kerth *et al.* 2006).

It is well-documented that there are fitness costs involved with increasing group size, including increased aggression and pathogen transmission (Krause & Ruxton 2002). Thus, individuals must balance consensus costs with grouping benefits (Conradt & Roper 2009) to decide between leaving the group, or abiding by the group's decision and following (Sueur *et al.* 2011). For example, because individuals might be unaware of the informational state of conspecifics (Conradt & Roper 2005), following a group member to a new patch increases uncertainty in foraging success – a classic risk-prone behaviour (Caraco 1981). At the same time, either decision will impact the spatial memory and spatial distribution of the individual (through whether or not they visit a new patch), providing information to potentially reduce uncertainty about future foraging options. For example, a follower may learn about a new patch location, and if it is a relatively good patch, the follower will continue to use it thereby leading to an adjustment in its space use pattern (Krebs & Inman 1992; Couzin & Krause 2003). Such a process is analogous to collective learning where social factors influence the environmental cue-reward relationship of associative learning (Kao *et al.* 2014). An individual who leaves the group, however, has the

option to return to a previously visited patch, resulting in restricted space use. The fitness benefits that encourage animals in fusion–fission societies to stay with, or leave a group during a disagreement are not well established (Sueur *et al.* 2011). Further, linking group decision-making processes with environmental heterogeneity should help determine the mechanisms governing restricted space use (Börger *et al.* 2008), and forecast animal distribution (Morales *et al.* 2010).

Our objectives were to (1) evaluate the role of individual knowledge during collective patch choice decisions, (2) determine under what circumstances animals might favour following other group members to a new patch, versus leaving the group and returning to a known patch, in situations where group member knowledge is conflicting, and (3) quantify the impact that following other group members to new places has on the spatial distribution of individuals. We examined these objectives using GPS radio-collar data collected between 2005 and 2014 from 22 free-ranging plains bison (*Bison bison bison*) residing in Prince Albert National Park (Canada). Bison forage in discrete meadow patches that are distributed in a forest-dominated landscape (Fortin *et al.* 2003). Decisions about which patch to visit next are closely linked to familiarity and maximising short-term energy gains; bison choose patches based on their expected mean profitability and whether or not they have previously visited them (Fortin *et al.* 2003; Dancose *et al.* 2011; Merkle *et al.* 2014). Bison live in an unstable fusion–fission society (Lott & Minta 1983; Fortin *et al.* 2009). Because the landscape is largely comprised of forest irregularly punctuated by meadows (3% of the land cover) connected by a network of trails (Dancose *et al.* 2011), bison groups do not move in averaged travel bearings but must make specific decisions about which patch to visit next (Fig. 1). Using field-derived measurements of expected energy gains as a fitness-based foraging currency, our work underscores the adaptive link between spatial memory and collective decision making in fusion–fission societies, and its ultimate impact on animal space use.

METHODS

Study area

Plains bison inhabit an area in and around the southwestern corner (ca. 1000 km²) of Prince Albert National Park, Canada

(53°44' N, 106°39' W). The study area has a cool sub-humid continental climate and receives a mean of 450 mm of precipitation annually. Mean daily temperatures range from −19 °C in January to +16 °C in July. The study area is characterised by aspen parkland in the south, and boreal forest in the north (see Fortin *et al.* 2003; Merkle *et al.* 2015 for details). During the study the bison population ranged 230–470 individuals (Merkle *et al.* 2015).

Animal locations

All analyses were based on relocation data collected every 3 h from GPS collared female bison within the park boundaries between 2005 and 2014. We captured and fit collars (4400M; Lotek Engineering, Newmarket, Ontario, Canada, and TGW 4780-3; Telonics, Mesa, AZ, USA) on adult (≥ 3 years old) females using a helicopter in winter. Fix rate of our GPS collars was $> 96\%$. Because we make inference about how past experience influences patch selection, we only used data from individuals monitored for > 1 year (i.e. the first year was used to quantify past experience). Because we make inference about group movement decisions, we only used data during periods when ≥ 8 bison were simultaneously monitored. Some individuals were monitored for > 2 years, and up to 4.

Role of individual knowledge during collective patch choice

To evaluate the role of individual knowledge during collective patch choice decisions, we developed a patch choice model to test whether focal collared bison selectively choose patches given that they, and other collared group members, had or had not previously visited them.

Determining group membership

At each 3 h location, we determined whether simultaneously collared individuals were in the same or different groups. Two collared individuals were considered in the same group when they were at a distance of ≤ 100 m from each other (Fortin *et al.* 2003). Because groups can become spread out while foraging in open areas and while traveling, we also allowed collared individuals to be > 100 m away from each other for up to 24 h, following the assumption that groups stay together for ca. 24 h (Fortin *et al.* 2009). Thus, collared individuals within a group could be > 100 m apart from each other as long as



Figure 1 A group of free-ranging plains bison in Prince Albert National Park moving towards the edge of a meadow. Note that not all individuals are moving in the same direction, indicating that a consensus in the travel direction towards the next patch has perhaps not been reached.

they were observed together (i.e. < 100) at least once before and after being apart, and the time that they were apart was < 24 h.

Model framework and development

Following the methods of Merkle *et al.* (2014), we developed patch selection models using an individual-based patch-to-patch movement framework (i.e. step selection function; Fortin *et al.* 2005). We identified a patch-to-patch movement as the last GPS location taken in one patch (i.e. source patch) and the first GPS location taken after entering a different patch (i.e. target patch). We identified patches as open areas (excluding roads) > 0.04 ha in size using a land cover classification derived from a SPOT5 multispectral image (taken in August 2008, 10 m resolution, accuracy = 89%; Dancose *et al.* 2011). For each patch-to-patch movement, we generated a sample of 20 potential target patches that the animal could have visited after departing the source patch. Potential target patches were chosen based on a distance probability proportional to the resource-independent movement kernel for bison. We established this distribution by estimating the shape ($k = 1.1$) and scale ($\lambda = 1.5$) parameters of a Weibull distribution using likelihood from the observed distances between the source and target patches of all patch-to-patch movements.

To take into account spatial attributes of patches known to influence bison movements (Dancose *et al.* 2011), we calculated log-transformed area of all patches, and for each patch-to-patch movement, the distance between the source and target patches. Then we calculated two variables representing focal animal knowledge and an index of the knowledge of other group members. First, for each patch-to-patch movement, we identified whether or not the focal animal had previously visited the target patch within at least the previous year. We did not take into account any effects of memory loss over time because in previous work we found minimal spatial memory decay in bison (Merkle *et al.* 2014). Second, we calculated the proportion of other collared animals within the group (excluding the focal animal) that had previously visited each target patch within at least the previous year. Because the index of other group member knowledge is based only on collared animals, it represents a sample of the entire group. Such a sampling regime is valid when two conditions are met. First, the collared animals must be a representative sample of the group. Accordingly, our capture efforts were conducted throughout the bison range to ensure broad sampling (Fortin *et al.* 2009). Furthermore, because bison live in an unstable fusion–fission society (Lott & Minta 1983), there is frequent mixing of the collared animals amongst groups. Second, the number of collared animals in a group must adequately represent group size. Indeed, the number of collared animals in a group is indicative of group size (see section on ‘Factors explaining when to follow versus leave group’ below), meaning that as the number of collared animals in a group increases, the proportion of the group that we sampled is consistent across observed group sizes. As an additional verification, we re-parameterised our model using only instances where ≥ 6 animals were collared during patch-to-patch movements. We found that results were not different, meaning that coefficient signs and significance were unchanged.

The first year of monitoring of each individual was used to quantify past experience and was thus not included in the analysis. Because some individuals were monitored for > 2 years and thus would have an inflated return rate, we identified a cut-off so previously visited patches could only be visited < 2 years in the past (i.e. patches previously visited > 2 years into the past were not considered past experience for a given patch-to-patch movement). Furthermore, we only used patch-to-patch movements for which ≥ 2 collared animals were in the same group in the source patch. Thus, our inference was based on a total of 9215 patch-to-patch movements by 22 individual female bison representing a mean monitoring time of 16.4 (SD = 8.1) months per individual and 37 unique individual-years between 2006 and 2013. Between the last GPS location taken in each source meadow and the first taken in each target meadow, group dynamics were as follows: stable (63%), new collared individuals joined group (i.e. fusion; 10%), some collared individuals left group (i.e. fission; 22%), and new collared individuals joined while others left (i.e. fusion and fission; 5%).

Parameterisation of patch selection model

We parameterised models by comparing used and available (i.e. potential) patches using conditional logistic regression. A stratum included the observed target patch and its associated 20 potential target patches. Because of temporal autocorrelation and a lack of independence within an individual’s patch-to-patch movements, we calculated robust SE and 95% CI of parameters using generalised estimating equations (Craaij *et al.* 2008). All strata for a given individual within a given year and season [spring (March–May), summer (June–August), autumn (September–November), winter (December–February)] were assigned a unique cluster (i.e. a total of 131 clusters). Model parameters were estimated using maximum likelihood in the survival package in R Version 3.1.0 (R Core Team 2014).

Factors explaining when to follow versus leave group

We identified potential conflict situations arising from when group members differ in their knowledge of the potential target patch (i.e. either the focal collared bison visited a new patch that other collared group members had previously visited, or there was a fission event during the patch-to-patch movement and the focal animal left other collared individuals to return to a previously visited patch). Using mixed effects logistic regression, these occasions were used to assess the circumstances that might favour decisions of whether to (1) stay with the group and follow to a new patch, or (2) leave the group and return to a known patch.

Using established theories of sampling behaviour, risk-sensitive foraging, and collective decision-making, we predicted that the choice to follow versus leave a group and return would be selectively advantageous under four circumstances: (1) when an individual’s local knowledge is insufficient to make a decision leading to a relatively high reward (*sensu* Lima 1984); (2) when group familiarity is high or when an individual can assume that collared group members have at least some information (King *et al.* 2011); (3) when an

individual has high local expectations (i.e. the source patch is relatively profitable) compared to the quality of its recent past experience (Merkle *et al.* 2014); and (4) when group size is relatively small, indicating that the benefits of grouping are becoming higher than consensus costs (Conradt & Roper 2009).

For each movement, we calculated: (1) local knowledge as the proportion of the focal animal's past locations that were within 6 km of the source patch (representing a radius covering 99% of the available patches), (2) group familiarity as the proportion of GPS locations of the focal individual collected prior to entering the source patch where the group composition (based on collared individuals) was the same as when the focal animal was in the source patch, (3) relative reference point as the mean profitability of previously visited patches discounted by time since entering the source patch and subtracted by the source patches' profitability (see Merkle *et al.* 2014 for calculation of the relative reference point), and (4) proportion of collared animals within a group as the number of collared animals within a group (range: 2–13 over the course of the study) divided by the number of collared animals monitored at that given time (range: 8–15). A random intercept was specified for animal id and year. Because patch profitability outside the park was not quantified, we removed patch-to-patch movements where the source or the observed target patch was outside the park, or when > 20% of available patches were outside the park (approx. 33% of the original database). We reran models with various cut-off points from 10 to 50%, and found that our choice of a 20% cut-off did not significantly affect the calculation of the reference point, and thus parameter estimates.

During summers 2006, 2012, and 2013, we examined whether proportion of collared animals within a group was indicative of group size. We systematically visited (3–6 times per week) meadows within the core bison range, and when individuals were found, we determined group size and the number of collared animals in the group using 10× binoculars and 60× spotting scopes. We observed a total of 155 groups, with a mean group size of 41.7 (SD = 28.4) individuals. During observations there were a mean of 11.8 (SD = 3.2) collared individuals on air, and we observed a mean of 2.5 (range: 1–10) collared individuals per group. Collared individuals represented a mean of 9% (SD = 10%) of the observed group size. We then calculated proportion of collared animals in each group (number of collars in group divided by number of collars on air; N_c), and found that this index was linearly correlated with group size: $\text{group size} = 10.5 + N_c \times 145.5$ ($R^2 = 0.56$, $F_{1,153} = 197.8$, $P < 0.0001$, $n = 155$).

Energetic benefits of following versus leaving group

Adaptive evolution is commonly used to explain the dietary choices of foragers. Indeed, the link between fitness and energy gains is a fundamental premise of optimal foraging theory (Stephens & Krebs 1986). Foraging decisions, residency time in meadows, and the distribution of plains bison is driven by the maximisation of short-term intake rate of digestible energy (Fortin *et al.* 2003; Babin *et al.* 2011). We thus used mean expected profitability (i.e. digestible energy/handling time;

Stephens & Krebs 1986) within patches to quantify the energetic benefits (a proxy for the adaptive value) of an individual's decision to follow versus leave the group compared to other locally available patches. We calculated mean expected profitability of each patch following methods outlined in Merkle *et al.* (2014, 2015). Mean expected profitability within patches does not change significantly after the passage of a bison group nor across years (Fortin *et al.* 2009; Merkle *et al.* 2015).

We first compared patch-to-patch movements resulting in the use of a new patch known only by other group members (thus unknown to the focal individual) to: (1) all other potential patches (random), and (2) patches known by the focal animal (return). We then compared patch-to-patch movements resulting in a fission and the focal animal returned to a previously visited patch to: (1) all other potential patches (random), and (2) patches unknown to the focal animal but known to others (follow).

For each of the four comparisons, we accounted for patch area and distance between source and target patch, while testing whether mean expected profitability of the chosen patch (*Profit*) was higher when either the focal animal followed or left the group, compared to the local options (indicating the choice was beneficial). We used conditional logistic regression, specifying strata and clusters as in the patch choice model parameterisation methods.

Impact of following on space use

To assess the influence that following other collared group members to new patches had on bison space use, we compared three spatial distribution metrics between all patches used by an individual over the course of a year with all patches subtracted by patches visited for the first time by following. To eliminate temporal biases, we only used individuals that were monitored for at least 11 months within a year (totalling 26 of the 37 animal-years). For each animal-year, we first identified all unique patches visited (i.e. all patches). We then identified which of those patches were not first visited by following (i.e. patches without following). Second, we calculated a utilisation distribution around all patches, and around all patches without following using kernel methods with a fixed smoothing factor calculated using the *ad hoc* method (Worton 1989). We calculated home range size as the area of the 95% contour of the kernels. Finally, we estimated percent change in the utilisation distribution by calculating the volume of intersection of the kernels estimated with all patches and patches without following (Fieberg & Kochanny 2005).

RESULTS

Role of individual knowledge during collective patch choice

While taking into account patch size and distance from source patch (Table S1), we found that focal bison used their personal knowledge and the knowledge of other collared group members to select foraging patches (Fig. 2). The odds (exponent of the beta coefficient) of choosing a target patch were highest when all collared group members had previously

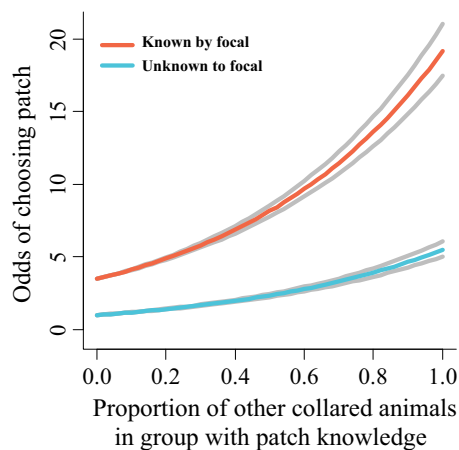


Figure 2 Odds of choosing a patch (with 95% CI in gray) depending on whether or not the focal animal or other collared group members have previously visited it (i.e. patch knowledge) during patch-to-patch movements by 22 female plains bison in Prince Albert National Park (Canada), 2006–2014. The model from which these predicted values were taken from also took into account patch size and distance between the target and source patch.

visited it. In addition, focal individuals selected patches that they had not visited but were previously visited by other collared group members (Fig. 2; Table S1).

Factors explaining when to follow versus leave group

We identified 1713 situations where focal animals either followed ($n = 1134$) or left the group and returned ($n = 579$). Focal bison tended to follow instead of leave the group when (1) in a group comprised of relatively familiar conspecifics, (2) their own local knowledge was poor, (3) their expectations were high given past experience (i.e. recent experience was of poor quality compared to the quality of the source patch),

and (4) in a group that was relatively small (although the latter trend was weak; Fig. 3; Table S2).

Energetic benefits of following versus leaving group

The choices bison made during conflict situations led them to patches of equal or higher profitability than expected given the local options. Specifically, leaving the group and returning resulted in the use of a patch that was more profitable than locally available options. Following group members resulted in the visitation of a more profitable patch compared to locally available random patches, and to a lesser extent, patches known by the focal animal (i.e. return; Fig. 4, Table S3).

Impact of following on space use

The mean number of unique patches visited by an individual bison during the course of a year was 243.2 (SD = 41.2) over a mean home range of 295.4 km² (SD = 47.1). A mean of 14.4% (range 4.8–26.1%) of those patches were first visited by following other collared group members. These new patches visited by following made up between 0 and 9% (mean = 3%) of individual annual home range size. The volume of intersection between the utilisation distribution with all patches and all patches subtracted by patches visited for the first time by following was on average 90% (range 86–93%), indicating that following led to a 10% change in the spatial distribution of an individual over a year. We do recognize that our estimates of the impact of following on space use are underestimated because we were unable to identify when focal individuals followed uncollared animals to new patches. Nevertheless, our results suggest that fusion–fission dynamics and the process by which group members handle conflicting information during decision-making can have a significant effect on the spatial distribution of individuals.

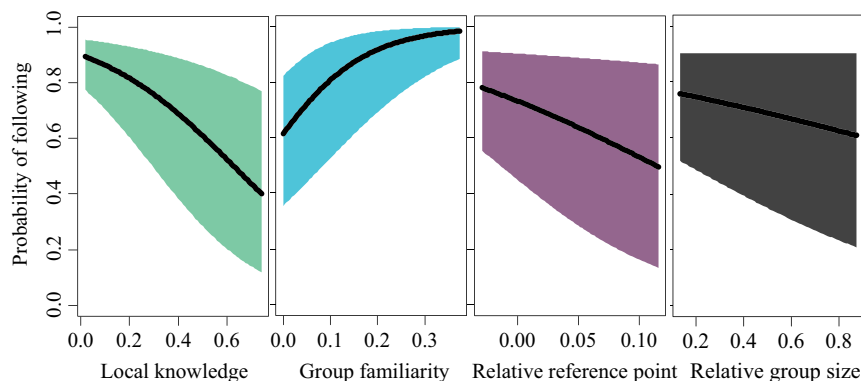


Figure 3 The probability of following (i.e. following a group to a new patch) as opposed to leaving the group and returning to a known patch during situations where an individual's knowledge conflicts with the knowledge of other group members. Predicted relationships (with 90% CI shaded) were derived from a mixed effects logistic regression model parameterised with GPS collar data from 22 bison in Prince Albert National Park (Canada) 2006–2014. Local knowledge is the proportion of time in past that the focal animal spent < 6 km of the source patch. Group familiarity is the proportion of time in past that the current collared group spent together. Relative reference point is an index of the focal animal's local expectations relative to mean profitability of recently visited patches. Relative group size is the number of collared animals within a group divided by the total number of collared animals monitored at the time.

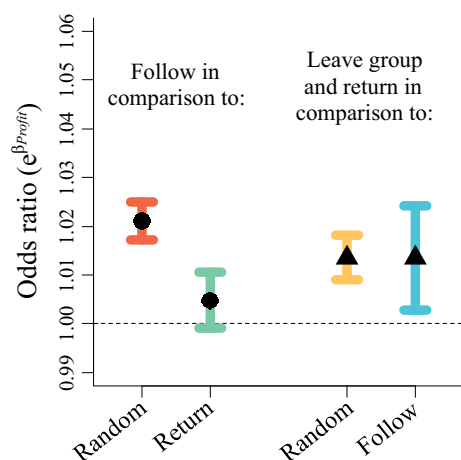


Figure 4 The odds (exponent of the beta coefficient for patch profitability [$e^{\beta_{Profit}}$] with 95% CI) of visiting a patch that is more profitable (i.e. expected kJ of energy per min) than available options (x -axis) when choosing to stay with a group and follow to a new patch known only by other collared group members (left panel), or choosing to leave group and return to a personally known patch (right panel). Estimates were derived from four models parameterised using conditional logistic regression from patch-to-patch movements of female bison ($n = 22$) in Prince Albert National Park (Canada), 2006–2014. Available options include: random, all potential patches; return, patches known only by focal animal; follow, patches unknown to the focal animal but known to others.

DISCUSSION

Group formation and the transfer of information among group members both play an important role in the space use dynamics of gregarious animals (Couzin *et al.* 2005). We demonstrate the adaptive advantages by which personal information and conspecific knowledge influences how individuals in fusion–fission societies choose between alternatives. Individual bison chose to follow other bison to new places over choosing random local patches based on the step length distribution of all bison, suggesting that following is a behavioural process that ultimately leads to the transfer of information among individuals about the location of high quality patches (Kerth & Recardt 2003). Furthermore, bison frequently chose the patch where all collared group members had previously been. Consistent with other findings, these results suggest that collective decisions in bison sometimes do not involve conflict and result in the option favoured by all group members (Conradt & Roper 2005; Petit & Bon 2010) even when there exists information heterogeneity (Couzin *et al.* 2011). In situations where group member knowledge about local foraging options was conflicting, bison chose to follow the group to a new patch over leave the group and return to a previously visited patch when basing foraging decisions on information known by others was beneficial (Fig. 3). Indeed, the decisions bison made during conflicts had adaptive value, resulting in the use of more profitable patches compared to other available options (Fig. 4). Information sharing thus has evolved as a way for individuals to minimise uncertainty in energy gains while foraging.

When information about local resource availability is lacking, individuals can use patch sampling behaviour (i.e. exploring new patches) to decide whether an area is worth returning

to in the future (Smith & Sweatman 1974). Although such sampling behaviour can be beneficial, it can also be risky. For example, the variance in the energy intake rate tends to increase while sampling until the animal obtains enough information to make an informed decision (Stephens 1987). For group-living species, individuals can also rely on the information of other group members to learn about local food availability without facing the same level of reduction in energy gains (Caraco 1981). For example, animals can obtain information about the quality of a patch by observing the foraging behaviour of others (Valone & Templeton 2002). However, when the informational state of conspecifics is difficult to discern, animals must depend on personal information to decide when it is beneficial to rely on conspecific knowledge (Miller *et al.* 2013). Our results suggest that using personal information (e.g. knowledge of local patch availability, recent past experience, familiarity with group) to decide when to rely on conspecifics and follow them to a new place is a risk-averse foraging strategy that can increase fitness by reducing uncertainty in energy intake rate. Our findings are indeed consistent with experimental trials of context-dependent group formation, where group members choose to merge together or break-up given their personal knowledge of potential food rewards or risk of predation (Hoare *et al.* 2004).

The personal information that bison appear to rely on also provides a possible mechanism for how leader–follower situations develop. Previous work on leadership emergence has demonstrated, for example, that individuals can become leaders because of their dominance status or because conspecifics recognise their knowledge (King & Cowlshaw 2009). In other cases, leadership can emerge without group members knowing who has relevant information. For instance, the state or motivation (e.g. thirst) of an animal will induce leadership (Rands *et al.* 2003). Compared to species living in stable groups, classic leader–follower situations (e.g. a matriarch female who always leads a group) should be relatively rare in fusion–fission societies (Fischhoff *et al.* 2007). Nevertheless, in some species certain individuals (e.g. older females) within groups still appear to lead group movements (McHugh 1958; Lewis *et al.* 2011; Sueur *et al.* 2011). Our results suggest a process for how such leadership emerges. We found that during conflict situations, an individual's personal knowledge influences their propensity to follow versus leave a group. Specifically, bison are more confident about their choice to leave a group and return to a previously visited patch when their recent experience is good and they are in a familiar area. Depending on the familiarity of the group and potentially the number of animals in the group, these individuals may more likely be followed. Hence, leadership develops without each individual knowing the informational state of others, but simply as a result of group members making decisions based on their personal knowledge (often referred to as distributed leadership; Leca *et al.* 2003). These findings are consistent with theoretical predictions where when individuals have meaningful personal information, they are more likely to discount social influence (Couzin *et al.* 2005, 2011). Furthermore, field observations confirm that bison groups often possess leaders, but leadership roles are not consistent over time (McHugh 1958). This adaptive, individual-based behavioural strategy

demonstrates how collective decisions are made, and why individuals in group-living species without a strong social structure can be observed as leaders in some cases but not in others (Lewis *et al.* 2011). Nonetheless, studies which directly monitor all group members would complement our work, and should provide a more comprehensive understanding of how leadership emerges in fusion–fission societies.

From an applied perspective, our finding that information can be transferred among individuals through collective decisions suggest that animal behaviour resulting in human–wildlife conflicts spreads more quickly through a population than would be expected by individuals that forage alone. For example, if a group of animals initially discovers rich forage on a farmland because of a random event (e.g. a long distance movement due to pursuit by a predator), collective decision-making will result in the relatively rapid transfer of this knowledge to new group members (*sensu*, collective learning; Kao *et al.* 2014). To avoid under predicting human–wildlife conflicts, models of animal space use would benefit from the inclusion of how group dynamics influence an individual's patch choice. For example, Morales *et al.* (2010) and Haydon *et al.* (2008) have outlined potential modelling frameworks to predict such group-influenced animal distribution. Furthermore, bison are classified as a threatened species in Canada (COSEWIC 2013), and their conservation is in part contingent upon successful predictions of population distribution. Future individual-based space use models for bison will benefit from taking into account not only abiotic and biotic factors (Fortin *et al.* 2003; Dancose *et al.* 2011) and individual past experience (Fortin 2003; Merkle *et al.* 2015), but also fusion–fission dynamics and information possessed by conspecifics.

Based on our results, we suggest three processes that can explain how fusion–fission dynamics shape animal space use dynamics. First, group-based information transfer, i.e. animals consistently learning about new sites by joining other groups with dissimilar knowledge, could be a mechanism by which animals learn about potential options and increase the overall quality of their home range. Second, because the amplification of beneficial information is expected to increase the frequency of favourable behaviour (Couzin 2009), information sharing should result, over time, in a stable core area of the best patches available. Indeed, bison in our study area spend the majority of their time in a core area encompassing only 10% (~ 100 km²) of their entire bison range (Merkle *et al.* 2015). Lastly, knowledge transfer of the best sites and the subsequent adjustment of individual behaviour to begin using them will generate intraspecific competition. For instance, public information about habitat quality can lead to conspecific attraction often resulting in overcrowding (Muller *et al.* 1997). In conclusion, our work demonstrates how fusion–fission dynamics affects information transfer and how natural selection has shaped a group-influenced behavioural strategy for coping with resource heterogeneity – both of which play a strong role in shaping animal distribution.

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AUTHORSHIP

DF conceived the original idea. All authors contributed to the study design. JAM conducted all analyses. JAM wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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