

Bison distribution under conflicting foraging strategies: site fidelity vs. energy maximization

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Abstract. Foraging strategies based on site fidelity and maximization of energy intake rate are two adaptive forces shaping animal behavior. Whereas these strategies can both be evolutionarily stable, they predict conflicting optimal behaviors when population abundance is in decline. In such a case, foragers employing an energy-maximizing strategy should reduce their use of low-quality patches as interference competition becomes less intense for high-quality patches. Foragers using a site fidelity strategy, however, should continue to use familiar patches. Because natural fluctuations in population abundance provide the only non-manipulative opportunity to evaluate adaptation to these evolutionary forces, few studies have examined these foraging strategies simultaneously. Using abundance and space use data from a free-ranging bison (*Bison bison*) population living in a meadow–forest matrix in Prince Albert National Park, Canada, we determined how individuals balance the trade-off between site fidelity and energy-maximizing patch choice strategies with respect to changes in population abundance. From 1996 to 2005, bison abundance increased from 225 to 475 and then decreased to 225 by 2013. During the period of population increase, population range size increased. This expansion involved the addition of relatively less profitable areas and patches, leading to a decrease in the mean expected profitability of the range. Yet, during the period of population decline, we detected neither a subsequent retraction in population range size nor an increase in mean expected profitability of the range. Further, patch selection models during the population decline indicated that, as density decreased, bison portrayed stronger fidelity to previously visited meadows, but no increase in selection strength for profitable meadows. Our analysis reveals that an energy-maximizing patch choice strategy alone cannot explain the distribution of individuals and populations, and site fidelity is an important evolutionary force shaping animal distribution. Animals may not always forage in the richest patches available, as ecological theory would often predict, but their use of profitable patches is dependent on population dynamics and the strength of site fidelity. Our findings are likewise relevant to applied inquiries such as forecasting species range shifts and reducing human–wildlife conflicts.

Key words: *Bison bison; density dependence; free-ranging plains bison; habitat selection; optimal diet; patch selection; population dynamics; Prince Albert National Park; Saskatchewan, Canada; site familiarity; site fidelity; step selection function.*

INTRODUCTION

Animals often face heterogeneity in the spatiotemporal distribution of resources, and the choice of where to forage can influence the spatial dynamics of consumer–resource processes. Optimal diet theory provides a theoretical baseline to understand how and why animals include prey items within their diet (MacArthur and Pianka 1966, Pulliam 1974). In landscapes where food patch quality is temporally stable, optimal diet models can be extended to understand optimal patch choice behavior (Pyke 1984). The theory predicts that foragers should choose patches yielding relatively high energy

intake rate, and, as the availability of the most profitable patches increases, less profitable patches should be excluded from an individual's home range (sensu Mitchell and Powell [2004]). Such an energy-maximizing patch choice strategy (i.e., do not choose a poor-quality site when a richer one is available) is an evolutionary stable habitat selection strategy (Pulliam and Caraco 1984, Pulliam 1989). In addition, developing site familiarity with patches and returning to them in the future (i.e., site fidelity) can also be a fitness-rewarding patch choice strategy. This benefit is particularly pertinent when consumers can develop familiarity with sites (e.g., acquiring means of efficient movement and effective escape from predators), and resources are temporally correlated (Switzer 1993, Piper 2011, Spencer 2012). For instance, in landscapes where patch quality does not always change over time, a “win–stay, or

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lose-switch" breeding habitat patch choice strategy will be adaptive (Switzer 1993, Schmidt 2001) and contribute to population persistence (Schmidt 2004).

Although both patch choice strategies (i.e., energy-maximizing and site fidelity) have adaptive value and should be simultaneously employed during periods when population abundance is increasing, a subtle yet important conflict develops between these strategies when population abundance is decreasing. In such a situation, individuals face a trade-off between two optimal behaviors: consistently choose patches that are familiar, or begin to avoid less profitable patches as interference competition for the most profitable patches declines. Although to our knowledge no study has examined how animals resolve this conflict, the first observations alluding to its importance were reported in birds. In an experiment investigating how territoriality influences density, Krebs (1971) found that experimentally creating vacancies in the best habitat did not always lead to Great Tit (*Parus major*) pairs switching out of poor-quality habitat. The replacements were first-year breeders without established territories, suggesting that established individuals were more likely to stay in their occupied site even when high-quality sites were available (also described by Piper [2011]). Similarly, O'Connor (1987) found that passerines in Britain, given a specific population density, inhabited a greater variety of nesting habitats during a period of population decline compared to a period of population increase. Despite these observations, however, the majority of research has focused on site fidelity and energy-maximizing strategies separately (Piper 2011). This is largely due to the reality that natural fluctuations in population abundance provide the only non-manipulative opportunities to evaluate adaptation to these evolutionary forces. Because both behavioral strategies can influence the space use of animals differently (Schmidt 2001, Bowler and Benton 2005), understanding how animals employ these conflicting strategies would help clarify the mechanistic and evolutionary link between fine-scale movement behavior, and population distribution and abundance (Morales et al. 2010).

Our objectives were to quantify how animals balance the trade-off between site fidelity and energy-maximizing patch choice strategies with respect to population abundance, and how these processes affect individual- and population-level spatial distribution. Using a behaviorally informed abundance model, we first clarified the increase and subsequent decrease in abundance of a free-ranging plains bison population (*Bison bison*) living in a forest-meadow matrix of Prince Albert National Park (Canada; see Plate 1). Second, we tested an essential assumption of the optimal patch choice framework (Pyke 1984). We verified that meadow quality (i.e., expected intake rate of digestible energy) does not change over short- (within a year) and long-term (across years) temporal scales. Thirdly, using a combination of aerial surveys, GPS collar data, and

field-based vegetation sampling, we examined how population range size, mean expected vegetation profitability of the range, and meadow selection varied over time. Consistent with the predictions of both patch choice strategies, we expected that, during the period of population increase, bison would expand into new areas with fewer and less profitable meadows, resulting in an increase in range size, and a decrease in the overall mean expected vegetation profitability of the range. During the period of population decline, according to the energy-maximizing patch choice strategy we expected that the probability of bison choosing the most profitable meadows would increase resulting in a decrease in the size of the bison range and an increase in the mean expected vegetation profitability of the range. In contrast, according to the site fidelity patch choice strategy during the period of population decline, we expected that the probability of bison choosing previously visited meadows would increase, due to an increasing likelihood that previously visited meadows are unoccupied, resulting in no change in the size of the bison range or in the mean expected vegetation profitability within the range. Finally, to assess how these patch choice strategies affect individual spatial distribution, we examined how individual variation in meadow selection behavior affects home range size. Since the population range in summer is smaller than in winter, resulting in contrasting population densities, we tested all predictions seasonally. By using a multi-scaled approach to understanding how density-dependent patch choice behavior can influence individual- and population-level animal distribution, our study provides a unique investigation of how site fidelity influences fitness-rewarding patch choice behavior.

METHODS

Study area

Plains bison inhabit the southwest corner of Prince Albert National Park (53°44' N, 106°39' W). The study area is characterized by long cold winters (January mean of -19°C) and short warm summers (July mean of +16°C), with the majority (~250 mm) of the 450 mm of annual precipitation falling as rain during summer. The overall bison range (approximately 960 km²) is characterized by aspen parkland in the south, agricultural fields in the west, and boreal forest in the north. Specifically, land cover types include deciduous (38%) and coniferous (37%) forest, pasture and agricultural land (11%), water bodies (5%), shrub (5%), meadow (3%), and road and bare ground (1%). Details of vegetation within the park can be found in Fortin et al. (2002).

Population abundance

To ensure that we had a natural experiment where abundance increased, then subsequently decreased, we estimated annual population size of bison throughout the study (1996–2013) using a generalized N-mixture

model (Royle 2004, Dail and Madsen 2011). The abundance model was parameterized in a Bayesian framework using JAGS (Plummer 2003) with data from annual aerial survey observations ($n = 18$ observations) collected in winter and parameter estimates of resource selection functions (Manly et al. 2002) from GPS collared female bison ($n = 46$ collared females). We then evaluated the posterior distributions of population size from the abundance model using a photographic mark-recapture technique (Merkle and Fortin 2014). See Appendix A for details of the GPS collar data, and on development, parameterization, and evaluation of the abundance model.

Temporal stability of meadow quality

To examine whether meadow quality (i.e., expected intake rate of digestible energy within meadows) is temporally stable, both within a year and across years, we surveyed vegetation within meadows before and after bison groups passed through meadows, and before and during the peak in population abundance. Fortin et al. (2009) reported that, on average, bison groups eat only 2% and 6% of the available biomass within a meadow during winter and summer, respectively. Using the same sampling technique, the functional response reported in Fortin et al. (2002) for bison, and the digestible energy of the eight most important plant species for bison reported in Courant and Fortin (2010), we calculated, in the summer of 2007 ($n = 34$ meadows), that mean expected profitability across a meadow decreases by only 2.3% after passage of a bison group. This value is likely an overestimate, because our analysis did not take into account that fact that bison are limited by digestive constraints, and they should be able to meet their voluntary intake rate by simply foraging longer during a day. Moreover, the overlap in foraging processes (Hobbs et al. 2003) should allow bison to maintain intake rate even with resource depletion (Fortin et al. 2002, 2004).

We examined long-term changes in expected profitability of meadows by comparing available vegetation in a sample of 20 meadows regularly visited by bison in 1997 and 1998 to 2008. We assessed vegetation in all three years in late summer (late July to August) using the sampling methods, functional response, and digestible energy estimates outlined in Fortin et al. (2002). We found no difference in the mean expected intake rate of digestible energy across the meadows between 1997 and 2008 ($t_{19} = 1.57$, $P = 0.13$) and between 1998 and 2008 ($t_{19} = 0.02$, $P = 0.99$).

Population range size and density

To examine how population range size varied over time, we calculated the size of the summer and winter range annually using GPS collar data ($n = 57$ collared females) and winter survey observations with kernel density methods (Worton 1989; see Appendix B for details). Because population abundance increased, then

subsequently decreased, we calculated change in range size by fitting piecewise regressions to the annual range size estimates. We forced a single breakpoint for the regression in year 2006 (i.e., just after the peak in population abundance; see Appendix D for detailed abundance estimates). For the GPS-based estimates, we used a weighted regression to account for range estimates where data were pooled across years with low sample sizes (see Appendix B for details). Using the resulting regression model, we extrapolated range size throughout all years of the study. We then calculated seasonal population density (abundance and range size) for each year using a bootstrapping approach (Efron and Tibshirani 1986), which took into account simultaneous variation in abundance and range size. For each year, we drew 10 000 abundance and range size estimates based on a Gaussian distribution with means as each estimated mean, and SDs as the estimate's SE. Trends in winter range size estimated using the GPS collar data were similar to range size trends from the aerial survey observations ($R^2 = 0.83$). We, therefore, only used range-size estimates from the survey observations for winter density calculations, because they were available for almost every year of the study.

Quality of population range

To test how the mean quality across the range varied over time due to fluctuations in range size, we calculated mean expected profitability (kJ of digestible energy per min) of the winter population range within the park each year. Expected profitability of each pixel within the range (including forested and non-vegetated areas) was calculated from a mathematical relationship between total aboveground dry biomass (based on field efforts) and the normalized difference vegetation index (NDVI) calculated from a SPOT5 image (10-m resolution; Dancose et al. 2011), and a quadratic relationship between mean total aboveground dry biomass and mean expected profitability within meadows (Merkle et al. 2014). Details of range quality calculation can be found in Appendix B.

Density-dependent meadow selection and home range size

We performed a seasonal analysis of patch selection (i.e., step selection function; Fortin et al. 2005, Dancose et al. 2011) by 33 radio-collared bison to investigate the influence of meadow profitability and past experience during the population decline period. See Appendix C for details on the development of the patch selection model. To assess the response of bison to meadow profitability, we assigned each target meadow (i.e., 1 case and 20 controls) its mean expected profitability value and area. We included meadow area as a potential covariate to expected profitability within meadows, because it has been shown to be relevant to bison during meadow selection (Dancose et al. 2011). To assess their site fidelity response, we also specified whether or not target meadows had been previously

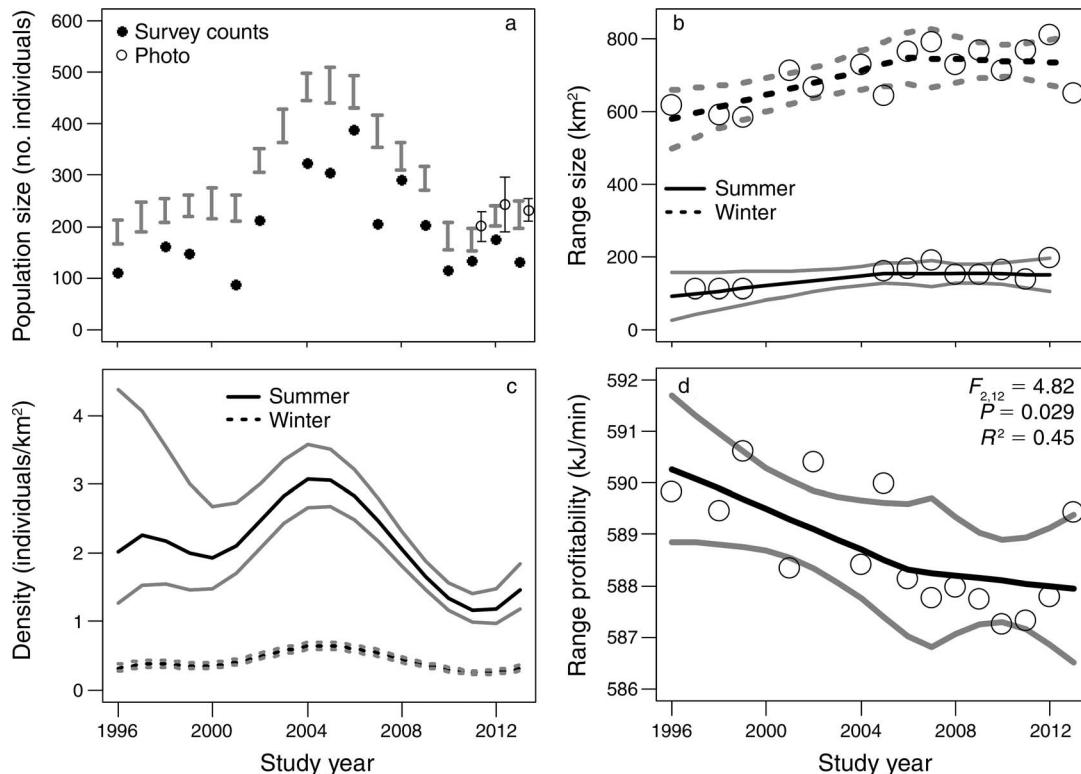


FIG. 1. Estimates of (a) population size, (b) seasonal population range size, (c) seasonal population density, and (d) mean expected profitability of the range over time for plains bison (*Bison bison*) in Prince Albert National Park, Canada, 1996–2013. Estimates were derived from a combination of GPS collar, aerial survey, photogrammetry, satellite imagery, and field-based vegetation data. In (a), gray error bars are posterior 95% confidence intervals (CI); black error bars represent 95% CI for the photo survey counts. In the other panels, gray lines represent 95% CI of estimates.

visited. Therefore, our patch selection model was based on relative profitability of target meadows (i.e., profitability of target meadow subtracted by source meadow; RelProfit), log-transformed area of target meadow (LogArea), distance between source and target meadow (Dist), and whether or not the target meadow was previously visited (Return). Prior to analysis, we removed the first three months of data for each individual to reduce false negatives regarding whether or not target meadows had been previously visited.

We parameterized the model using mixed effects conditional logistic regression (Duchesne et al. 2010) for summer and winter, separately. Random slopes were specified for all variables except Dist, representing each individual in each year. Parameters were estimated using maximum likelihood in the *coxme* package in R version 3.0.2 (R Core Team 2014). There was no multicollinearity among variables, as all variables had variance inflation factors < 2 . Variables were also centered and scaled to improve interpretability (i.e., ability to compare relative importance of variables; Schielzeth 2010).

Random slopes parameterized for each individual in each year allowed for a post hoc evaluation of the effect of density on meadow selection behavior. Using density

estimates and the corresponding individual random coefficients for a given year and season, we tested for relationships between density and annual variation in the probability of choosing profitable (RelProfit), larger (LogArea), and previously visited meadows (Return).

To assess how variation in meadow choice strategies affects the spatial distribution of individuals, we tested whether individual variation in random coefficients, for variables related to density, influenced seasonal home range size of individuals (see Appendix C for details on home range size estimation).

RESULTS

Population abundance

As indicated by the posterior probability distributions of our abundance model, population size ranged from a mean low of 174 in 2011, to a high of 474 in 2005 (Fig. 1a). Annual trends in population size clearly depicted an increasing population between 1996 and 2005 (mean geometric growth rate or $\lambda = 1.12$, SE = 0.04) and a decreasing population between 2005 and 2011 ($\lambda = 0.93$, SE = 0.06; Fig. 1a). The decrease in population size was due to a combination of an anthrax outbreak in 2008 (Shury et al. 2009), an increase in wolf presence beginning in the early 2000s, and an increase

in mortality due to hunting pressure outside of the park. Detailed results from the abundance model (including parameter and population size estimates, and bison sex and age structure) can be found in Appendix D.

Population range size and density

The size of the population range was up to five times larger during the winter than in summer, with a mean of 693.0 ± 57.5 and 140.0 ± 24.1 km² ($\bar{x} \pm$ SD) in winter and summer, respectively (Fig. 1b). Although bison expanded their range during the increase in abundance between 1996 and 2005 in winter ($\beta_{1996-2006} = 16.8$, SE = 4.8, $t = 3.5$, $P = 0.005$) and in summer ($\beta_{1996-2006} = 6.9$, SE = 2.7, $t = 2.5$, $P = 0.035$), we did not detect a decrease in range size after 2005 for both winter ($\beta_{2006-2013} = -18.6$, SE = 10.2, $t = -1.8$, $P = 0.093$) and summer ($\beta_{2006-2013} = -7.3$, SE = 5.0, $t = -1.5$, $P = 0.180$; Fig. 1b). Using mean range size estimates derived from best fit piecewise regression models, we found that mean bison density (individuals/km²) was 2.1 ± 0.6 ($\bar{x} \pm$ SD) for summer, and 0.4 ± 0.1 for winter (Fig. 1c). Population density increased by approximately 100% and 50% between 1996 and 2006 for winter and summer, respectively. After the peak, density during both seasons returned to levels >20% lower than population density during the mid-1990s (Fig. 1c), even though population abundance was similar (Fig. 1a). This difference in density, given similar abundances, was due to little or no decrease in the bison range after 2006 (Fig. 1c).

Quality of population range

Due to fluctuations in the size of the bison range, mean expected profitability of the range varied over time with an overall pixel mean \pm SD of 588.7 ± 1.1 kJ of digestible energy per min (Fig. 1d). Whereas range profitability decreased between 1996 and 2006 ($\beta_{1996-2006} = -0.2$, SE = 0.1, $t = -2.3$, $P = 0.042$), we did not detect a subsequent increase between 2006 and 2013 ($\beta_{2006-2013} = 0.1$, SE = 0.2, $t = 0.8$, $P = 0.450$). In other words, as the range size increased, bison used meadows and areas with a lower expected profitability, reducing mean profitability of the area of the bison range. After the population recovered, however, bison continued to use the same large range observed when population abundance was at its peak (Fig. 1).

Density-dependent meadow selection and home range size

Including random effects for each individual in each year improved both summer (integrated likelihood-ratio test $\chi^2 = 31962.5$, df = 9, $P < 0.0001$) and winter ($\chi^2 = 34483.6$, df = 9, $P < 0.0001$) meadow selection models, indicating significant variation in behavior among individuals and years. In both seasons, bison selected meadows that were previously visited, and meadows that were larger, closer, and of higher relative profitability than expected randomly (Table 1). The probability that bison chose a meadow they had previously

TABLE 1. Standardized parameter estimates of the summer and winter meadow selection model for free-ranging plains bison ($n = 33$ radio-collared bison) monitored with GPS collars in Prince Albert National Park, Canada, 2005–2013.

Variable	β	SE	z	SD of random β
Summer				
Return	1.221	0.035	34.730	0.008
RelProfit	0.216	0.020	10.690	0.003
LogArea	1.124	0.016	71.760	0.063
Dist	-0.215	0.014	-14.980	
Winter				
Return	0.757	0.038	20.170	0.136
RelProfit	0.503	0.027	18.920	0.094
LogArea	1.229	0.021	58.150	0.117
Dist	-0.932	0.019	-49.300	

Notes: Models were parameterized using mixed-effects conditional logistic regression, where random slopes were assigned to each individual in each year. Parameter estimates are shown for the relative profitability of target meadows (RelProfit), a log-transformed area of the target meadow (LogArea), the distance between source and target meadows (Dist), and whether or not the target meadow was previously visited (Return). Note that the 95% confidence intervals (CI) of all parameters do not overlap zero. Blank cells indicate that results were not applicable.

visited was related to annual variation in population density, with the strongest response observed in winter. In comparison to years of low density, during years of high population density (e.g., 2005 to 2008) individuals in winter visited more new meadows as their selection strength for previously visited meadows was lower (Fig. 2a). We found the same relationship, although weaker, in summer (Fig. 2b). We did not detect a relationship between population density and variation in the probability of selecting relatively profitable meadows (winter, $F_{1,61} = 0.64$, $P = 0.426$; summer, $F_{1,68} = 0.50$, $P = 0.483$) or larger meadows (winter, $F_{1,61} = 1.06$, $P = 0.306$; summer, $F_{1,68} = 1.16$, $P = 0.285$).

Based on GPS collar data collected between 2005 and 2013, home ranges of female bison were larger and more variable in winter ($\bar{x} = 365.1$ km², SD = 91.5) than in summer ($\bar{x} = 137.2$ km², SD = 26.0). During winter, individual bison that more strongly selected previously visited meadows also had smaller home ranges (Fig. 2c). However, we did not detect such a relationship during summer ($F_{1,65} = 0.56$, $P = 0.458$).

DISCUSSION

Our study reveals that an energy-maximizing foraging strategy alone cannot explain the distribution of individuals and populations. For bison, site fidelity appears to be a strong evolutionary force shaping their spatiotemporal range dynamics. During the period of population increase, bison used new areas with lower expected profitability. During the period of population decline, however, we found a clear departure from predictions of an energy-maximizing patch choice strategy. Range size and mean expected profitability of the range did not return to levels observed prior to

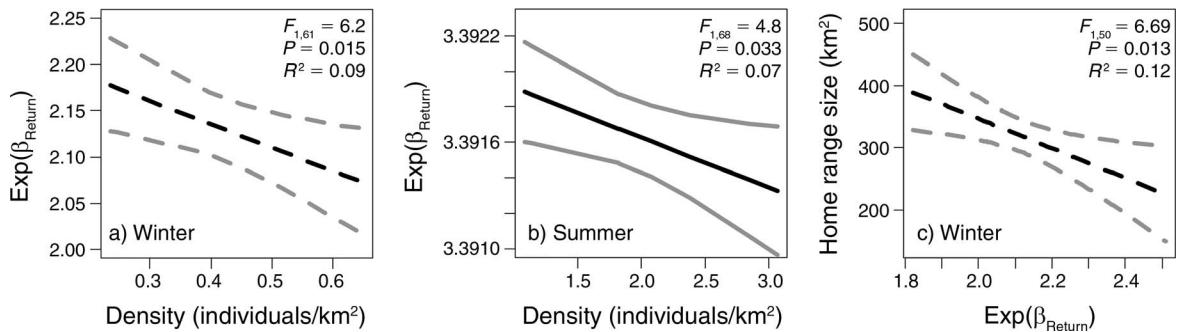


FIG. 2. Relative odds (exponent [exp] of the coefficient for return) of returning to a previously visited meadow in (a) winter and (b) summer as a function of winter and summer population density, and (c) winter home range size as a function of the relative odds of returning to a previously visited meadow for plains bison in Prince Albert National Park, Canada, 2005–2013. Lines represent predicted relationships using annual selection coefficients of each individual in each season, with gray lines representing the 95% CI of the prediction. Selection coefficients for each individual in each year were derived from a movement model for choosing which meadow to move to next.

the increase. We further found no evidence that the probability of choosing the most profitable meadows varied with population density. As density decreased, however, the strength of selection for previously visited meadows increased. As with similar observations (Krebs 1971, O'Connor 1987), bison behavior and distribution was more consistent with predictions of patch choice behavior driven by site fidelity. Moreover, individual variation in site fidelity was related to home range size, suggesting that the consequences of this fine-scale density-dependent patch choice strategy influence multiple scales of space use, impacting the overall spatial distribution of individuals and the population.

Observations of bison behavior outlined herein highlight the importance of incorporating past experience into foraging and movement models, and models of distribution and population dynamics. Classic theories such as the optimal diet model ignore past experience and assume foragers have complete knowledge of the energy gain related to every diet item (Pyke 1984). Other theories, such as models of how density-dependent site use influences population regulation are also predicated on the assumption that individuals always use the best sites available (Pulliam 1988, Rodenhouse et al. 1997), regardless of their past experience. Developing familiarity within a site, and thus site fidelity, however, offers advantages in dominance interactions (Kokko et al. 2006), learning the location of food (González-Gómez and Vasquez 2006), efficient movement in familiar space (Stamps 1995), and effective escape from predators (Brown 2001). Such non-energetic information, derived from an animal's past experience, can be beneficial for reducing uncertainty while foraging (Dall et al. 2005, McNamara and Dall 2010, Piper 2011). Although authors have suggested that such mechanistic ecological models should consider variables that represent past experience (Morales et al. 2010), researchers have only recently begun to integrate such covariates in

movement (Fagan et al. 2013), habitat selection (Wolf et al. 2009, Piper 2011), and animal distribution (Spencer 2012, Merkle et al. 2014) models. Further, models of how animals forage with incomplete information (e.g., Bayesian and risk sensitive foraging models) provide the theoretical baseline to understand the adaptive process by which foragers use information to maximize fitness benefits (McNamara and Houston 1992, Dall et al. 2005). Integrating information theory into the continued development of ecological models that incorporate an animal's past experience will prove fruitful for understanding the spatial dynamics of consumer-resource processes.

Variation in the size of individual home ranges can be explained by density-dependent effects on site fidelity and the propensity to explore new areas. During the peak in density (0.7 and 3.1 individuals/km² in winter and summer, respectively), the relative odds of an individual bison exploring new areas during meadow selection were between 5% and 10% higher, which ultimately resulted in a larger home range (Fig. 2). Such a relationship between fine-scale behavioral processes and home range patterns will have eco-evolutionary consequences, as lifetime reproductive success can be correlated with habitat components within a home range (McLoughlin et al. 2007). Mitchell and Powell (2004) hypothesized that the decision to add a patch to a home range is related to its resource value and how far the patch is from the core of the home range. Our work builds upon this model in two ways. First, we show that the decision to visit a patch is influenced not only by the patch's inherent quality, but also by whether or not the patch has been previously visited (Table 1; Merkle et al. 2014). Such site fidelity is certainly an important influence on the structure of a home range over time (Börger et al. 2008). Secondly, we show that when density-dependent factors (e.g., interference competition where animals more often occupy the most profitable sites) become evident, the propensity to



PLATE 1. A group of free-ranging plains bison foraging in a frequently visited meadow in Prince Albert National Park, Saskatchewan, Canada. Photo credit: J. A. Merkle.

disperse into new sites is higher (Matthysen 2005), a mechanism resulting in the development of a larger home range, and, ultimately, influencing population distribution through range expansion.

Our work supports theoretical predictions that the ability of animals to process and learn about their environment (i.e., acquire and update information) is a means to promote range expansion by adjusting behavior to marginal habitats (Sutter and Kawecki 2009). These adjustments can explain some of our observations. After bison expanded into new areas, they were faced with novel environments (e.g., smaller and fewer meadows containing different plant communities), which may have initially produced lower long-term averaged rates of food intake than in the core bison area. Bison likely adjusted their movement and group dynamics to learn about and exploit these new areas. Behavioral plasticity driven by past experience is essential to adapting to changing environments (Sih et al. 2004), and innovation (i.e., new, complex, or unusual behaviors) can provide animals with behavioral strategies that promote fitness in areas formerly thought to be of low quality (Reader and Laland 2003). Such flexible behaviors have even been suggested to be more prevalent during initial stages of colonizing a new environment (Wright et al. 2010).

The dynamics of a population's range boundary tend to be positively correlated with its abundance (i.e., the abundance–occupancy relationship; Gaston et al. 2000). This relationship would indeed be expected from density-dependent energy-maximizing patch choice behavior (Gaston et al. 1997). Yet, the evolution of a species' range through dispersal is influenced by genetics (e.g., gene flow from the core area), landscape characteristics (e.g., barriers), and distribution of conspecifics (reviewed in Holt 2003, Kubisch et al. 2014). In addition to these mechanisms, we demonstrate that past experience (through information use) also impacts a species' range and is particularly influential regarding the extent of a range retraction after a decrease in abundance. Fidelity to known sites could, therefore, decrease variation in range boundary dynamics, making it difficult to predict range retractions (Gaston et al. 2000). Correspondingly, such a mechanism potentially explains why management efforts to reduce population size and trigger a retraction of range distribution are often ineffective. For example, while culling of European bison (*B. bonasus*) in the Białowieża Forest of Poland has continued to take place, sustained range expansion has led to increasing human–bison conflicts (Hofman-Kamińska and Kowalczyk 2012). In situations where species are confined to certain areas (e.g., protected parks), and the expansion of their range may lead to human–wildlife conflicts (Naughton-Treves 1998), our

results suggest that reducing population abundance may not curtail dispersal beyond the protected area.

In conclusion, animals may not always forage in the richest patches available, as ecological theory would predict, but their use of profitable patches is dependent on population dynamics and the strength of site fidelity. The impacts of this site fidelity foraging strategy transcends scales of space use, affecting home range dynamics and population distribution. For basic ecologists, our results speak to a change in how we understand density-dependent patch choice behavior and its influence on animal distribution. Traditional measurements of site quality, such as energy gains, only explain a portion of the process, and an animal's familiarity (i.e., informational state) with a site has a profound influence on behavior (Piper 2011). For applied ecologists, the development of models that predict how animals interact with their environment will greatly benefit from integrating variables that denote the impact of site fidelity patch choice strategies. Ultimately, it is critical that individual-based models of habitat use incorporate how an individual's past experience will affect its subsequent behavior, as site fidelity is an important evolutionary force shaping animal distribution.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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