

The influence of winter severity, predation and senescence on moose habitat use

Robert A. Montgomery^{1,2*}, John A. Vucetich³, Rolf O. Peterson³, Gary J. Roloff² and Kelly F. Millenbah⁴

¹Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO, USA; ²Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, 48824, USA; ³School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI, 49931, USA; and ⁴Department of Fisheries and Wildlife, Lyman Briggs College, Michigan State University, East Lansing, MI, 48824, USA

Summary

1. Habitat use is widely known to be influenced by abiotic and biotic factors, such as climate, population density, foraging opportunity and predation risk. The influence of the life-history state of an individual organism on habitat use is less well understood, especially for terrestrial mammals.
2. There is good reason to expect that life-history state would affect habitat use. For example, organisms exhibiting poor condition associated with senescence have an increased vulnerability to predation and that vulnerability is known to alter habitat use strategies.
3. We assessed the influence of life-history stage on habitat use for 732 moose (*Alces alces*) killed by wolves (*Canis lupus*) over a 50-year period in Isle Royale National Park, an island ecosystem in Lake Superior, USA. We developed regression models to assess how location of death was associated with a moose's life-history stage (prime-aged or senescent), presence or absence of senescent-associated pathology (osteoarthritis and jaw necrosis), and annual variation in winter severity, moose density and ratio of moose to wolves, which is an index of predation risk.
4. Compared to senescent moose, prime-aged moose tend to make greater use of habitat farther from the shoreline of Isle Royale. That result is ecologically relevant because shoreline habitat on Isle Royale tends to provide better foraging opportunities for moose but is also associated with increased predation risk. During severe winters prime-aged moose tend to make greater use of habitat that is closer to shore in relation to senescent-aged moose. Furthermore, moose of both age classes were more likely to die in riskier, shoreline habitat during years when predation risk was lower in the preceding year.
5. Our results highlight a complicated connection between life history, age-structured population dynamics and habitat-related behaviour. Our analysis also illustrates why intraspecific competition should not be the presumed mechanism underlying density-dependent habitat use, if predation risk is related to density, as it is expected to be in many systems.

Key-words: Isle Royale, moose, pathology, predation, predator-prey, senescence, wolf

Introduction

Most research examining organism-habitat associations focuses on understanding how abiotic and biotic factors, including population density, influence habitat use (e.g. Pimm & Rosenzweig 1981; Morris & MacEachern 2010). Habitat use is also affected by an individual's vulnerabil-

ity to predation (Winnie & Creel 2007) which can change in response to the individual's body condition (Peterson 1977; Wright *et al.* 2006). These relationships suggest that habitat use may also be affected by an individual's body condition. Thus far assessments of such an effect on habitat use are rare (Heithaus *et al.* 2007).

Some fundamental changes in body condition over the lifetime of an individual are predicted by and understood through life-history theory (Mangel 2008). In particular, the life history of many organisms involves senescence.

*Correspondence author. E-mail: montg164@msu.edu

From a physiological perspective, senescence is the decline in body condition with increasing age (e.g. Doherty 2003). Within evolutionary ecology, this deterioration in condition ultimately results in a decline in vital rates. Much insight has been gained by understanding how senescence influences population dynamics (e.g. Nussey *et al.* 2008; Tuljapurkar, Steiner & Orzack 2009). Here we assess how habitat use, an important fitness-related behaviour (McLoughlin *et al.* 2006), is influenced by an important life history change for many species, the transition from prime condition to senescent. Shifts in habitat use due to changes in body condition or life-history stage are thought to generate complicated population dynamics and community-wide consequences for at least some aquatic invertebrates and marine reptiles (Heithaus *et al.* 2007; McCoy, Barfield & Holt 2009). However, similar connections are not well understood, especially among terrestrial mammals. Moreover, assessing such connections in mammals is difficult because variation among life-history stages for mammals tend to be less pronounced than those of, for example, many invertebrates.

Wolf-ungulate systems are especially well suited for examining how senescence affects prey vulnerability and corresponding habitat use. For instance, the presence of wolves (*Canis lupus*) causes ungulates to use habitat that offers better protection from predation (Creel *et al.* 2005) and ungulates in poorer nutritional condition seem to use different habitats than individuals in better nutritional condition (Winnie & Creel 2007). These patterns may be attributable to wolves' tendency to selectively kill senescent ungulates (Wright *et al.* 2006).

Here we endeavour to better understand how habitat-related behaviours might be influenced by factors such as senescence, predation risk and winter severity. Our analysis involves the assessment of spatio-temporal patterns in the locations of wolf-killed moose carcasses observed over a 50-year period on Isle Royale, an island in Lake Superior, USA. Using the locations of predated individuals to infer general aspects of habitat-related behaviours is far from ideal and poses two significant limitations. First, habitat use throughout an individual's life likely differs from habitat use immediately preceding death, although there is good reason to think the two processes are related (McLoughlin, Dunford & Boutin 2005). Secondly, spatio-temporal patterns in the locations of such carcasses are the combined result of not only habitat use by the moose, but also predatory behaviours of wolves and the relative predation risk experienced by various kinds of moose in different habitat types.

Despite these limitations, two features of this data set seem to make such an analysis worthwhile. First, few studies have assessed how habitat-related behaviours change in response to varying environmental conditions throughout a five-decade period, even though variation over such time-scale is important (Beyer *et al.* 2010). Second, and more importantly, few studies can assess the potential influence of life-history condition on

habitat-related behaviours of a mammal. Such studies are rare precisely because it is difficult to observe the habitat-related behaviours of a living mammal and also know its age and body condition.

Study system

We evaluated winter habitat use of moose living in Isle Royale National Park (544 km²), an island ecosystem in Lake Superior, USA. The moose population is typically comprised of 700–1100 individuals (1.4–2.4 km⁻²) (inter-quartile ranges) (Vucetich, Peterson & Schaefer 2002). During most winters, wolf predation accounts for more than 80% of moose deaths (e.g. Vucetich & Peterson 2011), and the mean annual predation rate for the moose population (> 9 months of age) is 9.9% (Vucetich *et al.* 2011). Growth rate of the moose population is negatively influenced by severe winters (Vucetich & Peterson 2004) and high rates of predation (McLaren & Peterson 1994; Wilmers *et al.* 2006; Vucetich *et al.* 2011). Neither wolves nor moose have been subjected to human hunting pressure.

The shoreline habitat of Isle Royale is characterized by conifer-dominated forests (i.e. *Abies balsamea*, *Picea glauca* and *Thuja occidentalis*) which moose prefer in winter (Puttock, Shakotko & Rasaputra 1996; Jordan, McLaren & Sell 2000; see Appendix S1 in Supporting Information). With increasing distance from the shore, deciduous species (especially, *Populus spp.*, *Acer spp.*, and *Betula spp.*) become more common (Krefting 1974; Jordan, McLaren & Sell 2000). Because Isle Royale moose prefer *A. balsamea* and *T. occidentalis* during winter (Vucetich & Peterson 2005), habitat closer to shore represents the best of the available foraging opportunities, with consideration for predation risk, energy expenditure and forage intake (Geist 1982; Edwards 1983; Peterson & Page 1993). Conifer-dominated forests are also associated with lower snow depth, which favour moose mobility, and greater horizontal structure of vegetation, which favour escape from predation (Peterson 1977). These habitat characteristics are associated with moose density being greater in habitat that is closer to the shore (e.g. Vucetich & Peterson 2011). However, wolves also travel and forage more frequently in shoreline habitat (see Appendix S2 in Supporting Information). Thus, habitat near to the Lake Superior shore provides moose with better forage, but may also correspond to riskier habitat. For these reasons, distance to shore represents important changes in habitat for both moose and wolves on Isle Royale.

Field methods

Between 1959 and 2008, we found and necropsied the carcasses or skeletal remains of moose that had been killed by wolves during winter (Fig. 1). Most carcasses were located during aerial surveys that tracked the movement of wolves through the snow during a 7-week

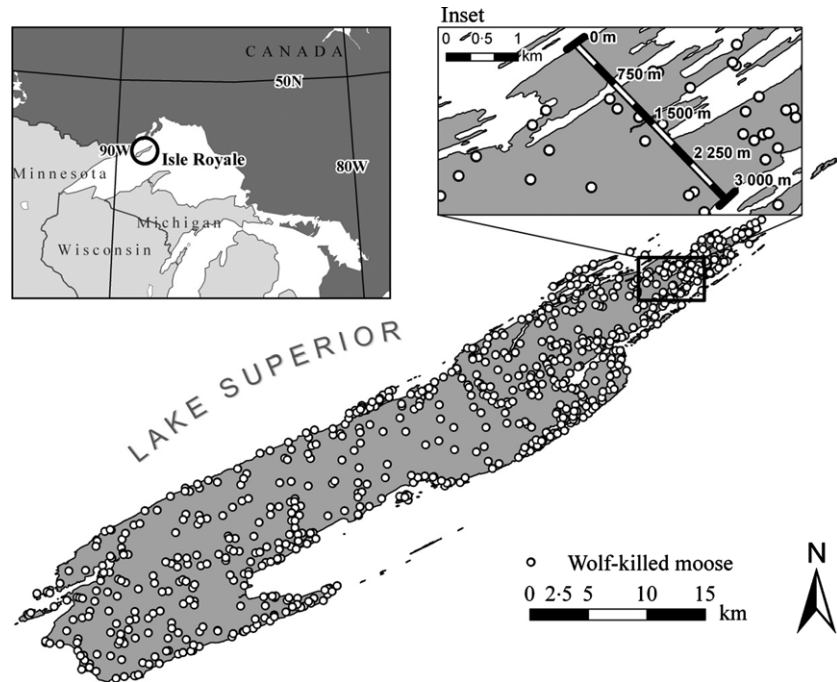


Fig. 1. The location of Isle Royale National Park within Lake Superior (upper panel) and the distribution of moose killed by wolves during the winter ($N = 732$) in Isle Royale National Park, USA, 1959–2008. The inset provides a scale to help interpret the response variable depicted as the y -axis of Fig 2 and 3.

field season conducted each January and February. Some additional carcasses were also discovered during summer ground surveys that involved extensive off-trail hiking. Because most carcasses in this sample were located from light fixed-wing aircraft in conjunction with estimating kill rate, few moose that died during the field season were missed (Vucetich, Peterson & Schaefer 2002). For carcasses discovered in winter, necropsies were conducted as soon as possible after wolves finished feeding on a carcass and left the area, typically within 7 days of the moose's death (Vucetich, Vucetich & Peterson 2012).

Necropsies included inferring the cause of death from field sign (e.g. blood on trees, signs of a chase and signs of struggle including broken branches). For carcasses discovered during the summer, season of death was also inferred from field sign (e.g. degree of decomposition, presence of adult ticks that exist only in winter or early spring). From the necropsies, we identified sex, we estimated age at time of death by counting annual cementum lines in the teeth (Bubenik 1997) and we recorded osteoarthritis (Peterson *et al.* 2010) and periodontal disease (Peterson 1977) as being absent, mild, moderate or severe.

The location of each carcass was recorded by GPS after 2002, and on aerial photographs (scale $\sim 1 : 18000$), prior to 2002. The accuracy of these carcass locations is necessarily high, given the context [i.e. the range of distance from Lake Superior shore is (0, 5.4 km)]; because a carcass located from the air must also be found, on a later date, by a ground crew, for the purpose of conducting a necropsy. Locating a carcass from the ground in a dense forested environment requires the aerial observer to plot locations accurately and precisely. Carcass locations are

also representative of habitat use in the days prior to being wolf-killed because moose make daily movement decisions at relatively small scales (10–100's of meters) (Phillips, Berg & Siniff 1973) and chase distances of wolves for moose tend to average < 100 m (Wikenros *et al.* 2009).

We used GIS to calculate the distance of each carcass to the shoreline of Isle Royale. Moose killed by wolves on Lake Superior ice were assigned a distance value of 1 m, meaning that they were considered to be on shore. In the majority of these cases, the moose would have been on the shoreline and chased onto the ice by wolves.

Analysis

Our analysis was designed to understand whether a moose's propensity to be in habitat that was closer to the shore, where forage quality and predation risk are greater (see *Study System*), was influenced by the moose's age or temporal variability in predation risk and winter severity. In particular, we used generalized linear models and generalized linear mixed models (R Development Core Team 2012) to assess whether the response variable, which was the location of a wolf-killed moose carcass quantified as distance from shore, was associated with any of these predictors: two biotic covariates (ratio of moose to wolf abundance and moose density), one abiotic covariate [North Atlantic Oscillation Index (NAO)] and three individual body condition covariates (sex, age class and pathologic condition). We standardized the continuous predictors to have a mean value of 0 and a standard deviation of 1 to facilitate comparison of the regression coefficients. The gamma distribution with an identity link was necessary to achieve homoscedastic residuals, which is not

surprising given that the response variable was limited to positive values and the variance of the response increased with its value. Using model selection techniques described in Zuur *et al.* (2009), we also evaluated the need for autocorrelated error terms and a random effect term for year. The inclusion of these terms did not improve model performance, so they were not included.

The ratio of prey to predator (RATIO) is a useful predictor of predation rate (Vucetich *et al.* 2011), which is a population-level measure of predation risk (i.e. the proportion of moose killed annually). Ungulate density (MOOSE) is an important indicator for a variety of density-dependent processes including intraspecific competition for forage (Patterson & Power 2002; Vucetich & Peterson 2004). Winter severity and its effect on ecological processes are complicated. Consequently, large-scale, seasonal indices of climate spanning several months can be better indicators of winter severity than local climatic factors for ungulate populations (Hallett *et al.* 2004). In particular, NAO is an index of winter severity for many ungulate populations (Ottersen *et al.* 2001), including Isle Royale moose (Vucetich & Peterson 2004). We used annual NAO values reported by Hurrell (1995) and annual estimates of moose and wolf abundance reported in Vucetich *et al.* (2011).

We categorized moose as prime-aged if they were 1–10 years old and senescent-aged if they were > 10 years old (AGE). This classification corresponds to the age when survival and reproduction begin to decline in moose (Ericsson & Wallin 2001; Ericsson *et al.* 2001; Vucetich & Peterson, unpublished data). We categorized moose as pathologic if they exhibited either of two senescence-associated pathologies (PATH). Specifically, a moose was categorized as pathologic if it exhibited moderate or severe periodontal disease and/or moderate or severe osteoarthritis. Moose were otherwise categorized as non-pathologic. Because moose habitat use commonly differs between sexes (Dussault *et al.* 2005), we also included sex as a predictor covariate (SEX).

Our model building procedure was based on nine predictor variables; three individual body condition predictors (AGE, SEX and PATH) and three environmental predictors (RATIO, MOOSE and NAO) that could be assessed for their influence during the current year (t) and the previous year ($t-1$). Before building any models, we assessed the collinearity of the predictors. Because RATIO and MOOSE exhibited enough correlation to be of concern ($R = 0.79$; $P < 0.01$, see Dormann *et al.* 2012), we did not evaluate any models that included both RATIO and MOOSE.

We first assessed which of the three body condition covariates were significant predictors of the location of wolf-killed moose. Backward elimination indicated that AGE was significant, while SEX and PATH were not. Next we assessed how the influence of AGE might be modulated by environmental covariates. To do so, we examined the interaction terms that included AGE and

each of the environmental predictors for year t or $t-1$. We assessed the interactions in two rounds so that RATIO and MOOSE were not considered simultaneously. This application of backward elimination indicated that $\text{RATIO}_{t-1} * \text{AGE}$, $\text{MOOSE}_{t-1} * \text{AGE}$ and $\text{NAO}_t * \text{AGE}$ were important interaction terms. The candidate models that we assessed represented every possible combination of those retained predictors. Thus, we evaluated a total of 20 models (see Table 1 for the top 10-ranking models). We compared these models using Akaike's Information Criterion (AIC) and ranked model performance with AIC weights (AICw) (Burnham & Anderson 2002).

Results

Between 1959 and 2008 aerial and ground surveys located 732 winter wolf-killed moose for which we could assess age, sex and pathology (periodontal disease and osteoarthritis; Fig. 1). Among this data set, 309 were males, 423 were females, 340 were not pathologic, and 392 were pathologic. Furthermore, 347 moose were prime-aged and 385 moose were senescent-aged. Prime-aged moose died, on average, more than 200 meters farther from shore than did senescent moose ($t = 2.20$, $P = 0.01$). The difference is ecologically significant because small differences in distances from the shoreline correspond to substantial shifts in habitat and predation risk due to the biogeography of Isle Royale (Fig. 1, Fig. S1).

The most parsimonious model, as judged by AIC, included AGE ($P = 4.97 \times 10^{-4}$), RATIO_{t-1} ($P = 2.00 \times 10^{-16}$), NAO_t ($P = 2.37 \times 10^{-5}$) and $\text{NAO}_t * \text{AGE}$ ($P < 0.01$; Table 1). This model indicates that moose tended to die closer to the shore, where foraging opportunities were better and predation risk was likely greater, when the ratio of moose to wolf abundance (i.e. predation risk) had been lower in the preceding year (Fig. 2). The interaction term of $\text{NAO}_t * \text{AGE}$ indicates that the effect of winter severity in year t on habitat use depended on the age class of the moose (Table 2). Specifically, prime-aged moose had a tendency to die farther from shore during mild winters and much closer to shore during severe winters (Fig. 3a). By contrast, senescent-aged moose habitat use changed little in relation to winter severity (see coefficients in Table 1). However, when the influence of RATIO_{t-1} is ignored, senescent-aged moose tended to die farther from shore during severe winters (Fig. 3b).

Because MOOSE_{t-1} and RATIO_{t-1} are related (both statistically and in their interpretation, see below), there is value in considering the best performing model that predicted carcass location from MOOSE_{t-1} . While that model is less parsimonious ($\Delta\text{AIC} = 3.4$), it does clearly suggest that moose die farther from shore when moose density is high ($P = 1.37 \times 10^{-9}$). This model also indicates that senescent-aged moose tended to die farther from shore during severe winters (see coefficients in Table 1 and Fig. 3b).

Table 1. Rankings of the top-10 models developed to evaluate the habitat selection of moose in relation to the Lake Superior shore in Isle Royale National Park, USA, 1959–2008. Coefficients significant at $\alpha = 0.025$ level are highlighted in bold-type face

Rank	Coefficient (SE)									
	AIC	Δ AIC	AICw	AGE	RATIO _{t-1}	MOOSE _{t-1}	NAOI	RATIO _{t-1} * AGE	MOOSE _{t-1} * AGE	NAOI * AGE
1	11345.7	0.0	0.53	-276.36 (79.00)	-223.14 (20.42)		169.66 (39.88)			-140.44 (43.47)
2	11347.2	1.5	0.26	-232.45 (93.87)	-200.40 (35.68)		187.22 (48.66)			-161.17 (54.94)
3	11349.1	3.4	0.10	-338.08 (83.70)			158.01 (45.16)			-170.66 (45.99)
4	11350.1	4.4	0.06	-284.53 (95.98)			188.65 (55.49)			-215.04 (66.91)
5	11352.0	6.3	0.02	-208.92 (75.83)	-214.48 (22.05)		69.54 (25.92)			
6	11354.0	8.3	0.01	-204.77 (93.50)	-185.91 (49.32)		60.94 (26.03)			
7	11354.8	9.1	0.01		-220.40 (22.30)		103.32 (27.75)			
8	11355.8	10.1	0.00		-109.17 (63.82)					
9	11356.0	10.3	0.00		-216.11 (23.54)					
10	11356.0	10.3	0.00							-222.59 (18.56)

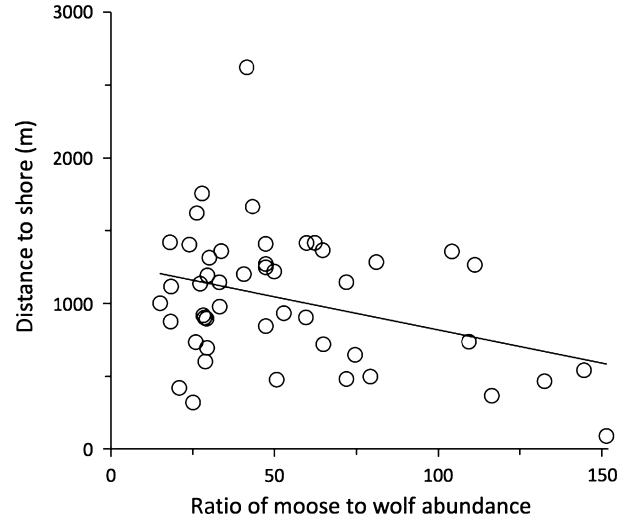


Fig. 2. The influence of predation risk, indexed by the ratio of moose to wolf abundance in year $t-1$, on the location of wolf-killed moose in relation to Isle Royale's Lake Superior shore. Observations represent the mean location for each year of the study period (1959–2008). The line is a simple linear regression ($P = 0.02$, $R^2 = 0.12$), fit to the data depicted in this graph. The inset in Figure 1 offers a basis for interpreting the scale of the y-axis. Low values of RATIO correspond to high predation risk.

Discussion

The tendency for prime-aged moose to die farther from shore than senescent moose certainly represents a difference in habitat-related behaviour. The development of more specific inference requires care. In particular, the location of wolf-killed moose results from two processes: (i) wolves selecting habitat for hunting; (ii) moose using habitat that balances predation risk and foraging opportunities (Bergman *et al.* 2006). With the available data, the two processes cannot be disentangled. If, however, both processes are important, then it is fair to conclude that the differences in carcass locations arose in part from differences between senescent and prime-aged moose in their use of habitat. Because the habitat available to these groups of moose was at least largely overlapping (i.e. senescent and prime-aged moose can be found on any portion of Isle Royale), then differences in kill locations may also be reflective of differences in habitat selection. Regardless of whether the results reflect differences in selection (in addition to differences in use), the observations represent interesting differences in habitat-related behaviours.

The second point of care required for drawing inferences from these data is that while habitat use throughout an individual's life is certainly related to habitat use immediately preceding death, the two processes are not identical (McLoughlin, Dunford & Boutin 2005). Thus, the results readily support the inference that senescent and prime-aged moose exhibit different habitat-related behaviours at the time directly preceding their death. The data do not, however, provide a basis for judging whether this difference is manifest at other times of individuals' lives.

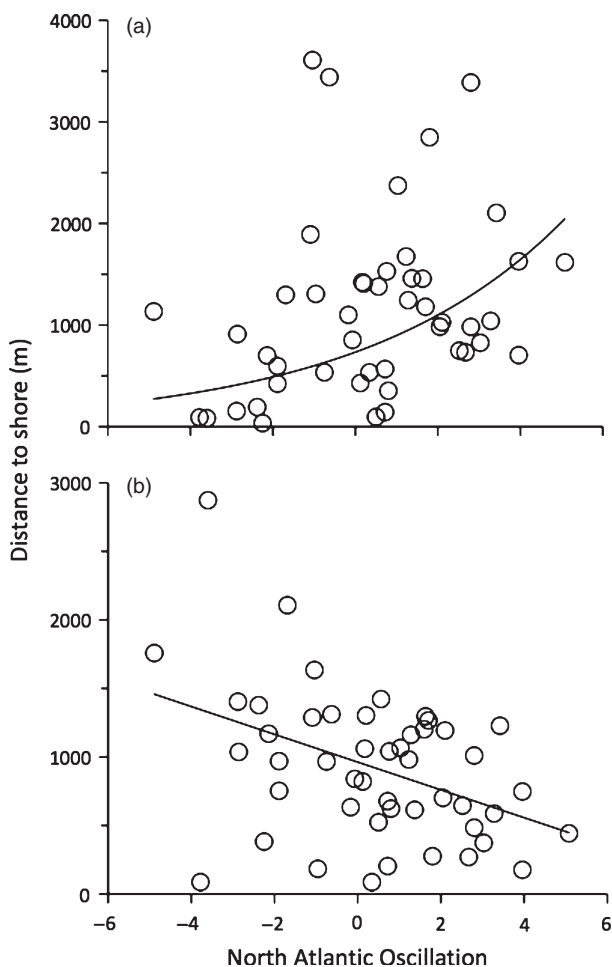


Fig. 3. The influence of winter severity, indexed by the North Atlantic Oscillation (NAO) in year t , on the location of wolf-killed moose in relation to Isle Royale's Lake Superior shore. Panel (a) represents prime-aged moose and panel (b) represents senescent-aged moose. Observations represent the mean location for each year of the study period (1959–2008). The lines are regressions fit to the data depicted in these graphs. Panel (a) is an exponential curve ($P = 2.00 \times 10^{-3}$, $R^2 = 0.19$) and panel (b) is simple linear regression ($P = 3.10 \times 10^{-3}$, $R^2 = 0.17$). The inset in Figure 1 offers a basis for interpreting the scale of the y-axis. Low values of NAO represent more severe winters.

Nevertheless, parsimony suggests it is at least plausible that the differences arose well before the time of death.

In principle, habitat use of an herbivore should depend on its vulnerability, given prevailing habitat and environmental conditions. While there are many aspects to environmental conditions, habitat and moose vulnerability, our analysis seems to have detected the influence of some of these aspects and their interaction. In particular, prime-aged moose, compared to senescent moose, tend to make greater use of habitats farther from shore, where predation risk is less, but so are foraging opportunities. However, severe winters changed the behaviour of prime-aged moose. In severe winters, prime-aged moose tend to make greater use of habitats that are closer to shore, where foraging opportunities and predation risk are greater (Fig. 3a). By contrast, senescent-aged moose

decreased their use of near-shore habitat in severe winters (Fig. 3b). These patterns suggest that prime-aged moose may be less sensitive to the modulating effect of severe winters on predation risk (cf., Figs. 3a and 3b). This result is more complex than theoretical models which predict that animals in poor condition (e.g. a hunger state) are expected to be riskier in their pursuit of quality forage (McNamara & Houston 1986).

The frequency of senescent individuals in a population varies over time and among populations. That variation influences important population-level processes including per capita kill rate (Peterson *et al.* 2010) and growth rate (Coulson *et al.* 2001). Our work suggests that a population's age structure may also affect habitat use, which could in turn influence spatial patterns in ecosystem processes such as herbivory and nutrient cycling (Bump, Peterson & Vucetich 2009; De Jager & Pastor 2009). Dynamic habitat use, like that observed here, also has to potential to stabilize age-structured population dynamics (Bowers 1994). While the details of such relationships remain under-evaluated, our work provides some critical elements for understanding how interactions between life history and habitat-related behaviours might influence population-level processes (Morris 2003a).

Interpreting the relationship between ratio of prey to predator and the location of wolf-killed moose (Fig. 2) is challenged by the strong correlation between ratio (RATIO) and prey density (MOOSE). Before assessing that challenge, consider a naïve interpretation that ignores the correlation. In particular, during years following low values of the ratio of moose to wolves (high predation risk), moose of both age classes tended to die closer to shore (Fig. 2). This result suggests that moose tend to use habitat in *places* that have better foraging opportunities and greater predation risk at *times* when predation risk had been low in the previous year. That is, the moose responded to risky times and places (Creel *et al.* 2008).

Elk (*Cervus elaphus*) have been shown to exhibit short-term shifts in habitat use with daily variation in predation risk, as determined by the immediate presence of wolves (Creel *et al.* 2005). The results presented here further suggest that temporal variation in predation risk also affected ungulate habitat use on annual time scales. If habitat-related behaviours are more sensitive to recent predation risk than current predation risk, as suggested by the time lag associated with ratio of moose to wolves, then the risk perceived by moose may be as important as actual risk (Zanette *et al.* 2011). The lagged behavioural response is also important for its potential to affect population stability (Luttbeg & Schmitz 2000).

Predation risk varies tremendously among individuals (Pettorelli *et al.* 2011). Some of that variation is captured by differences in age class, and some by differences in carcass locations (e.g. Fig. 3). The remaining variation in predation risk among individuals is not accounted for by the available data. Even in the presence of what must be considerable variation in predation risk among individuals

at any point in time, temporal variation in predation risk (averaged across the population) also appears to influence the central tendency of habitat-related behaviour.

RATIO is a good index of predation rate ($r = -0.62$, $P < 10^{-3}$), largely because predation rate is the kill rate multiplied by the inverse of that ratio. However, predation rate on Isle Royale is inversely density dependent. Consequently, prey density is also a useful index for predation rate ($r = -0.64$, $P < 10^{-3}$). For this reason, it is not surprising that moose of both age classes also tended to die closer to shore when moose abundance was low (model 10 in Table 2). The interpretive challenge lies in not knowing what density represents. If prey density represents the strong density-dependent nature of predation, then the interpretation given above is appropriate. However, the results might represent density-dependent habitat use, driven by intraspecific competition. In that case, habitat use observed during periods of low density (low values on x -axis of Fig. 2) represents more preferred habitat, compared to habitat use when density is high (Clutton-Brock, Iason & Guinness 1987; Ramp & Coulson 2002; Møbak *et al.* 2009). As such, moose would seem to prefer the habitats on Isle Royale with greater foraging opportunity, but greater predation risk, compared to the habitats with lower risk and lower foraging opportunity. Competition and predation risk are both likely to be important influences on habitat use in most real systems. However, the joint influence of these processes are rarely studied together, and theory suggests that the dynamics of such interactions are quite complex (Morris 2003b, 2009).

This interpretive challenge represents an underappreciated challenge for much work on density-dependent habitat use. Specifically, intraspecific competition should not be the presumed mechanism underlying density-dependent habitat use, if predation is related to density, as is expected to be the case for many systems. Where predation is strongly linked to density, isolating the relative influence of predation risk and intraspecific competition on habitat use would require not letting density be a surrogate for anything, but instead to more directly assess predation risk and intraspecific competition for resources.

Wolves have long been considered to be highly selective in their pursuit of prey (Mech 1970, Wright *et al.* 2006). Our work further suggests that wolves not only have the ability to select for individuals with various body conditions within the prey population but they also have the ability to target these individuals in environmental space. Thus, our study substantiates that wolf hunting patterns correspond to the habitat decisions of their primary prey (Jedrzejewski *et al.* 2001, Bergman *et al.* 2006; Kauffman *et al.* 2007). Our results also suggest that the interaction of moose life-history state with winter severity may be, in part, a product of wolf hunting tendencies. For instance, per capita kill rates by wolves tend to be greatest during severe winters (Nelson & Mech 1986, Huggard 1993, Hebblewhite, Pletscher & Paquet 2002). This tendency is likely associated with moose nutritional condition and

their corresponding ability to forage (Gasaway *et al.* 1983). Consequently, the habitat decisions of moose are a complex dynamic that likely depends on climatic conditions, their body condition, as well as wolf hunting strategies.

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Author Contribution Statement

R.A. Montgomery was the project leader who developed and executed every aspect of the entire analysis. J.A. Vucetich assisted the analysis through the generation of the question, the collection of the data and the write-up of the manuscript. R.O. Peterson assisted with the generation of the question, the collection of the data and the write-up of the manuscript. G.J. Roloff assisted with the generation of the question, methodological development and the write-up of the manuscript. K.F. Millenbah assisted with the generation of the question, methodological development and the write-up of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Maps representing the spatial distribution of moose abundance per km² across Isle Royale based on winter aerial surveys conducted in 1990, 1995, 2000, and 2005.

Appendix S2. The distribution of wolf tracks in 1 m² sections of Isle Royale based on winter aerial surveys conducted in 1980, 1985, 1990, 1995, 2000, 2005, and 2010.