Selecting habitat to what purpose? The advantage of exploring the habitat–fitness relationship

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Abstract.   Measures of reproductive success have been recognized in many fields as essential tools to assess the status of populations, species, and communities. However, difficulties in gathering data on reproductive success often prevent researchers from taking advantage of the information offered by those measures. For example, most of habitat selection studies do not include reproductive success in their analysis even though doing so would highly improve our understanding of the habitat selection process. In our study, we aimed to assess to what extent habitat selection choices made by adult individuals are directed to increase their annual reproductive success. We tested this idea by first developing habitat selection models and then relating the results of those models to two measures of reproductive success. Using wolves, *Canis lupus*, as the study species, we determined that not all habitat selection choices performed by adult wolves were related to their annual reproductive success. The results varied also in relation to the measure of reproductive success used in the analysis and other individual-, group-, and population-level factors. Likely, adult female wolves select habitat characteristics to increase not only their annual reproductive success but also their lifetime reproductive success, for example, by ensuring their own survival and reproductive abilities in subsequent years. Our study suggests that a variety of motivations may govern habitat choices performed by adult individuals and including different measures of fitness in habitat selection studies can improve our understanding of these complex processes.

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Introduction

Fitness is an essential concept in evolutionary ecology and presumed to be important in shaping observed patterns of habitat selection (McLoughlin et al. 2006). One of the most direct indicators of fitness is lifetime reproductive success (LRS). Because LRS is difficult to measure, the relationship between habitat selection and LRS has been

evaluated on only two occasions (McLoughlin et al. 2006, 2007). McLoughlin et al. (2007) observed a strong relationship between LRS and home range selection (i.e., second-order habitat selection; Johnson 1980). McLoughlin et al. (2006) assessed that density dependence had a strong mediating influence on the relationship between LRS and third-order habitat selection (Johnson 1980). Both studies focused on ungulate

species and assessed selection for habitats characterized by vegetative community, for measures of habitat quality are expected to be tightly linked to the foraging success of herbivores.

Because LRS is difficult to measure, it is more common, though still rare, to evaluate whether and how habitat selection is associated with either of two basic components of fitness, survival and short-term reproductive success (RS). For example, habitat selection of woodland caribou (*Rangifer tarandus caribou*) was associated with survival, but the relationship was mediated by predation risk and the temporal scale at which survival was estimated (DeCesare et al. 2013).

Evaluations of the importance of habitat selection on realized fitness are also exemplified by numerous assessments of the relationship between nest site selection for birds and some aspect of RS, for example, nest survival (Badyaev 1995, Aldridge and Boyce 2007, Sandercock et al. 2015, Gibson et al. 2017). The collective impression of those studies has been characterized as "equivocal" (Bloom et al. 2013). The equivocal results of those studies are likely, and in part, the consequence of two complicating circumstances. First, RS itself has several components, not all of which would be equally important to overall LRS or fitness. Second, important trade-offs exist between components of fitness. For example, in certain circumstances, animals may favor individual survival over RS (Arlt and Pärt 2007). Therefore, patterns of habitat selection may be directed to benefit one (unobserved) component of fitness, rather than another (observed) component.

On only two occasions (to our knowledge) has habitat selection in a carnivore been associated with components of fitness. The purpose of the first study (Mosser et al. 2009) was to determine whether three measures of habitat quality for Serengeti lions (*Panthera leo*) at the territory level (i.e., second-order habitat selection; Johnson 1980) were equally effective to detect good-quality habitats, described by six landscape variables expected to be indicators of habitat quality for lions. The three measures of habitat quality were (1) RS measured as yearling cubs produced by lion prides, (2) a population-level measure of RS (yearling cubs per km^2), and (3) population density measured as individuals per km^2. The two measures of RS were more successful than population density in detecting good-quality habitat. The second

study (Rauset et al. 2015) was also based on the analysis of second-order habitat selection and aimed at determining the link between habitat selection and a measure of RS, that is, the number of weaned cubs produced annually by female wolverines (*Gulo gulo*). They determined that resource availability had a stronger effect on RS of prime-age females that had produced cubs in the previous year than on younger or older females.

Current knowledge of habitat–fitness relationships can be summarized as follows: Habitat–fitness relationships are likely important, but also liable to be complicated by density and other population- and individual-level phenomena, the component of fitness being measured, and trade-offs among components of fitness. More precise understandings will require additional assessments on different kinds of systems. Here, we assess the association between third-order habitat selection (i.e., habitat selection within a home range; Johnson 1980) and two measures of RS for female wolves (*Canis lupus*).

The study of the relationship between habitat selection in wolves and their RS may provide interesting insights on this topic because of the essential differences between reproductive strategies of ungulates, birds, and carnivores, concerning the mobility of their young. In ungulate species, the calf can potentially follow its mother hours after been born. In many bird species, the chicks spend a proportionally long time in the nest before they are ready to leave it, and soon thereafter, they reach independence. In most carnivore species, pups are kept in the den for a short period of time, followed by a period in which they start following the adults for short trips, but are not completely independent for a long time after den emergence (see, e.g., Ausband et al. 2016). Therefore, third-order adult habitat selection, that is, the habitat visited by the adult caring for the young, has a different value for each of those groups. In herbivores, the habitat chosen by the mother is directly essential to calf survival, because it influences at the same extent detectability by predators and food availability. In birds, detectability by predators is mainly determined by the habitat characteristics of the nest, while adult habitat selection regulates food availability. In carnivores, adult habitat selection controls food availability for the offspring from birth to independence, while it likely influences their safety

from predation (or intraspecific attacks) at different degrees throughout the offspring development. In the early stages of development, the habitat characteristics of the den are most important. When the young start following the adults, but only for brief trips away from the den, both habitat at the den site and habitat selected by the adults are important. Finally, when the young follow the adults in all their movements, habitat selection of the adults becomes vital. Therefore, the strength of the relationship between habitat selection and RS in carnivores is likely intermediate compared to ungulates and birds.

As mentioned above, previous studies have determined that second-order habitat selection is related to RS in carnivores (Mosser et al. 2009, Rauset et al. 2015); that is, the most successful individuals occupy the best-quality territories. Third-order habitat selection is also likely related to RS. Indeed, habitat selection within the territory boundaries is related to hunting success (Hopcraft et al. 2005, Balme et al. 2007, Kauffman et al. 2007), and it likely influences the ability of the adults to hide and protect their pups from fatal attacks by predators or conspecifics. However, the relationship between third-order habitat selection and RS in carnivores has yet to be assessed.

The purpose of our study was to determine to what extent third-order habitat selection of adults in a carnivore species is related to their RS, and whether this relationship is mediated by other individual features that are known to affect RS. In the case of wolves, those features are female age, body size, and coat color, pack size, conspecific abundance, and whether the pack was affected by diseases (Stahler et al. 2013).

Methods

Study area

The YNP ecosystem hosts a variety of large carnivore and herbivore species, including wolves, grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Puma concolor*), elk (*Cervus elaphus*), bison (*Bison bison*), moose (*Alces alces*), and mule deer (*Odocoileus hemionus*). Elk constitute 90% of the wolf diet in the northern part of the park, while in the central and southern areas wolves prey mainly on elk in the summer and switch their diet to bison in the winter (Smith et al. 2004). Grasslands and shrub steppes dominate valley bottoms, which constitute favorable habitat for wolf rendezvous sites (Mech 1970, Ballard and Dau 1983, Arjo and Pletscher 2004). Lodgepole pine (*Pinus contorta*) forests are also dominant in the park. Additional tree species include aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) (Despain 1990). For a detailed description of the study area, we refer the reader to the extensive literature published from the park (see, for example, Metz et al. 2012, Uboni et al. 2015*a*, *b*).

Data collection

Since wolf reintroduction in YNP in 1995–1997, movement and reproductive data have been collected every year from some individuals in each wolf pack, as part of the monitoring program of the Yellowstone Wolf Project. We used spatial locations collected from May 1997 to December 2008 from 19 breeding female wolves monitored with very high frequency (VHF) collars (for details on wolf capture, collaring, and monitoring, see Smith et al. 2004, Metz et al. 2012, Stahler et al. 2013). Locations from collared females were collected weekly during most of the study period, with an effort of collecting one location per day from mid-November to mid-December every year. These locations are not temporally autocorrelated because in 24 h wolves have the ability to visit any part of their territory (Mech 1970). Each year we recorded the number of pups at den emergence (in May) and the number of pups that survived to the end of the year (December 31). Female wolves were not considered in the analysis in years when they did not produce pups or no alive pups emerged from the den. The sample unit was female/yr, leading to 33 observations, each one representing one female wolf (19 in total, belonging to 15 different packs) and one pup-rearing season. Although usually the wolf pup-rearing season in North America is defined as the period going from April to September (Mech and Boitani 2003), in this study we considered the pup-rearing season to be the period May through December. In May, pups start emerging from the den (Young and Goldman 1944), and by January, some pups are beginning to disperse (Fuller 1989, Gese and Mech 1991, Mech and Boitani 2003). Telemetry locations were subsampled to cover only the pup-rearing season.

Table 1. Predictor variables included in the resource selection functions used to describe female wolf habitat selection from May to December in Yellowstone National Park.

Variables	Type	Description
Elevation (*elev*)	Continuous	Elevation in meters. $elev^2$ indicates a squared term for elevation
Slope (*sl*)	Continuous	Slope in degrees
Openness (*open*)	Continuous	Percentage of open habitat (developed by Mao et al. 2005)
Distance from rivers (*riv*)	Continuous	Euclidean distance from major watercourses (>20 km in length), in meters
Distance from roads (*rd*)	Continuous	Euclidean distance from primary roads in meters. rd^2 indicates a squared term for *rd*
Distance from edge (*edge*)	Continuous	Distance in meters from edge between forest and open areas
Vegetation type (*veg*)	Categorical	Vegetation type divided into six categories: developed, herbaceous, forest, shrub, water, and wetland. For details on how the six categories were defined, see Uboni et al. (2015*a*)

Statistical analyses

Overview.—The aim of our study was to determine whether the habitat selection exhibited by a female wolf influences its pups' survival. To reach this aim, we followed the two-stage modeling approach proposed by McLoughlin et al. (2006): (1) describe the habitat selected by adult females and (2) link habitat selection to RS. In the first stage, we developed resource selection functions (RSFs) to describe female wolf habitat selection (see the *Resource selection functions* subsection below). As in McLoughlin et al. (2006), we did not employ RSFs for statistical inference, but as estimating functions. The regression coefficients from the RSFs (βs) can be used as a basis to detect links between habitat selection and RS. In particular, the second stage of our analysis consisted of building regression models where a measure of RS was treated as the response variable and the βs obtained from the RSFs were candidate predictor variables (see *Linking habitat selection and reproductive success* subsection below).

Resource selection functions.—Resource selection functions predict the relative probability of use of a certain habitat compared to all available habitats in an animal's home range (Manly et al. 2002). Paired logistic regression model was used to estimate each RSF. Each location used by a female wolf in a certain pup-rearing season was paired to five randomly selected locations representing the habitat available in its territory (Arthur et al. 1996, McCracken et al. 1998, Cooper and Millspaugh 1999). In other words, we assessed third-order habitat selection (Johnson 1980). The available locations were selected to be specific to the time and space at which used locations were collected (McCracken et al. 1998). More specifically, the

pup-rearing season territory was defined for each female/yr by combining the summer and early winter territories developed by Uboni et al. (2015*a*, *b*) for each female's pack. Then, random locations were selected inside the territory boundaries using the "genrandompnts" function in the Geospatial Modelling Environment 0.7.3.0 (Beyer 2014) and ArcGIS 10.1 (ESRI 2012). Used locations falling outside the territory boundary were discarded from the analysis. Each used location was assigned a value equal to 1 and each available location a value equal to 0. This binomial variable was the response variable in our logistic regression models.

The habitat and topographic characteristics considered as predictor variables are listed in Table 1. They are the same that were used in Uboni et al. (2015*a*), plus an additional "distance from *edge*" variable. This variable was included because Bergman et al. (2006) identified it as an important component of wolf hunting strategy. The *edge* map was developed starting from the vegetation-type map used in Uboni et al. (2015*a*). Following Nelson et al. (2012), all vegetation types were combined into two categories: open and forest. Mixed, deciduous, and evergreen forests and woody wetlands belonged to the "forest" category, while all other vegetation types were classified as "open." Starting from this reclassified map, a map representing the edge between the two vegetation categories and then a raster indicating the distance to the closest edge were developed. Because adult wolves select habitat in YNP based on elevation and distance from roads in a nonlinear manner (see Uboni et al. 2015*a*), we tested quadratic terms for those variables in the RSFs.

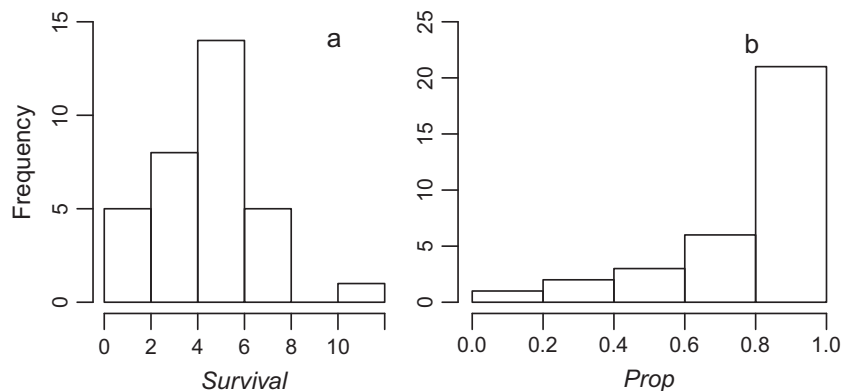For each female/yr, we selected the best-fit model using bidirectional stepwise elimination,

Fig. 1. Histograms representing the frequency distribution of reproductive success of female wolves in Yellowstone National Park from 1997 to 2008. Data include 33 female/yr. Reproductive success is represented as the number of pups survived to December 31 in panel (a) (*survival*), and as the proportion of pups survived to December 31 in panel (b) (*prop*).

run with the function *stepAIC* available in the MASS package in R 3.2.5 (Venables and Ripley 2002).

Linking habitat selection and reproductive success.—After obtaining RSFs for each female/yr, we extracted the regression coefficients (βs) related to each habitat variable. These coefficients became the candidate predictor variables in a new regression model, where the response variable was *survival*, which we define as the total number of pups produced by a female in one year that survived to the end of the year. For habitat variables not included in the best-fit RSF models, the coefficient was set to 0. To account for how *survival* might also be influenced by other unmeasured factors, we evaluated several random-effect terms, representing *Year*, *Female ID*, and *Pack ID*. These variables might explain variance in *survival* associated with, for example, properties of individual females (e.g., personality), properties of individual packs (e.g., culture), and properties of particular years (e.g., adverse meteorological conditions). While *survival* is a count variable, the data did not follow a Poisson distribution (Fig. 1a). Therefore, we ran linear mixed-effect models, using the *lme* function in the nlme package for R 3.2.5 (Pinheiro et al. 2016). The residuals of those models followed a normal distribution and had constant variance. On the basis of Akaike Information Criterion (AIC, Burnham and Anderson 2002), *Pack ID* was the only random term to improve model performance. Further evidence for the importance of

this random term is that its standard deviation was higher than the residual standard deviation. For all subsequent analyses, we included *Pack ID* as a random term.

Next, we used the *dredge* function in the MuMIn package for R 3.2.5 (Barton 2016) to generate models predicting *survival* for all possible combinations of the candidate predictors, where the candidate predictors were the regression coefficients of the RSFs. We judged model performance on the basis of *P*-values and AIC corrected for small sample size, AIC_c (Burnham and Anderson 2002). We gave consideration to models with ΔAIC_c values less than two (Burnham and Anderson 2002).

We also evaluated models of *survival* that focused on the possible interaction between habitat selection and several variables demonstrated to be important for the fitness of wolves (Stahler et al. 2013), that is, female age, body size, coat color (black or gray), pack size, conspecific abundance, and whether the pack was affected by canine parvovirus in that specific year. Body size was age-specific and estimated in kg with a growth model developed by Stahler et al. (2013). Pack size referred to the number of adult wolves in the pack counted in March. Conspecific abundance was derived by counts conducted on the YNP wolf population in December of the previous year, that is, prior to whelping. For additional details on these fitness-related variables, see Stahler et al. (2013). We tested each fitness-related variable separately to avoid over-parameterizing

Table 2. Best-fit regression models ($\Delta AIC_c < 2$) predicting reproductive success from habitat selection.

| Resp | Model | Predictor variables | | | | | | df | logLik | AIC_c | ΔAIC_c |
		sl	open	riv	rd	rd^2	herb				
Survival	M1	14.2*	−93.3**	20.1	0.2**	−0.2**		8	−64.08	150.2	0
	M2		−64.5*		0.2**	−0.2*		6	−67.82	150.9	0.71
	M3	12.0	−78.6**		0.3**	−0.2**		7	−66.35	151.2	1.01
	M4		−75.3**	17.0	0.2*	−0.2**		7	−66.49	151.5	1.3
	M5		−80.9**		0.2**	−0.2*	0.1	7	−66.74	152	1.79
	M6				0.2*			4	−71.36	152.2	1.99
Prop	Ma	12.5*				−0.2*		4	−46.43	102.3	0
	Mb	15.8*			0.1	−0.2**		5	−45.73	103.7	1.39
	Mc					−0.1*		3	−48.65	104.1	1.84

Notes: Reproductive success is quantified in two different ways: (1) *survival*, which is the number of pups survived to the end of the year and (2) *prop*, which is the proportion of pups survived to the end of the year. The predictor variables are coefficients obtained from parameterizing resource selection functions (Appendix S1: Table S1). Abbreviations associated with habitat selection variables are defined in Table 1. "*herb*" stands for the herbaceous category of the vegetation-type variable. The *survival* models are Gaussian mixed-effect models, while the *prop* models are binomial mixed-effect models. *Pack ID* was included as a random-effect term in all models. For each predictor variable, the table reports regression coefficients and significance levels, which are expressed as $^*P \leq 0.05$ and $^{**}P \leq 0.01$. Resp = response variable; df = degrees of freedom; logLik = log-likelihood; AIC_c = Akaike Information Criterion corrected for small sample size; ΔAIC_c = difference in AIC_c compared to the best-fit model.

the models. Each candidate model included (1) *Pack ID* as a random term, (2) all RSF coefficients detected as significant explanatory variables in the procedure described above, (3) the fitness-related variable, and (4) interaction terms between the fitness-related variable and the RSF coefficients. We ran linear mixed-effect models, using the *lme* function in R (R Development Core Team 2016). Then, we used the *dredge* function and followed the same selection procedure described above to detect the best-fit models.

We repeated the regression analyses described above, using a different measure of RS as a response variable, that is, *prop*, which is the proportion of pups that emerged from the den in May to have survived to the end of the year. For example if 10 pups emerged from a den but only five survived to year's end, then RS = 0.5. This measure of RS is useful for relating the habitat choices during the pup-rearing season (May–September) to pup survival, without regard for the number of pups that emerged from the den. Furthermore, *prop* was not related to the number of pups that left the den (Appendix S1: Fig. S1). Because *prop* is a proportion and not normally distributed (Fig. 1b), we used the *glmer* function in the lme4 package for R 3.2.5 (Bates et al. 2015) to relate *prop* to the RSF coefficients and to test the interaction between RSF coefficients and fitness-related variables through generalized mixed-effect

models (GLMMs) with logit function. Because the model that aimed at testing the interaction between coat color and RSF coefficients failed to converge, we tested the interaction between coat color and each RSF coefficient separately.

RESULTS

The average (±SD) number of pups that emerged from the den was 6.1 (±2.4) pups per female. The average number of pups survived to the end of the year was 4.7 (±2.3), corresponding to a coefficient of variation (CV) = 0.48 (Fig. 1a). The average proportion of pups survived was 0.81 (±0.26), CV = 0.32. 52% of the female/yr had a RS = 1 (Fig. 1b).

Patterns of habitat selection were variable among females, as well as among years when considering the same female in different years (Appendix S1: Table S1). The *open* variable was retained in 82% of the 33 RSFs, *elev* in 73%, *riv* in 42%, *sl* and *rd* in 39%, *edge* in 30%, and *veg* in 24%.

Of the regression models relating *survival* to the RSF coefficients, six had ΔAIC_c values <2 (Table 2). The top model indicated that variation in pup survival was explained by the selection of habitat based on slope, openness, and distance from rivers and roads (model M1 in Table 2, Fig. 2). *Open*, *rd*, and rd^2 were included in five of these six top-performing models, and *rd* was included in all six models.
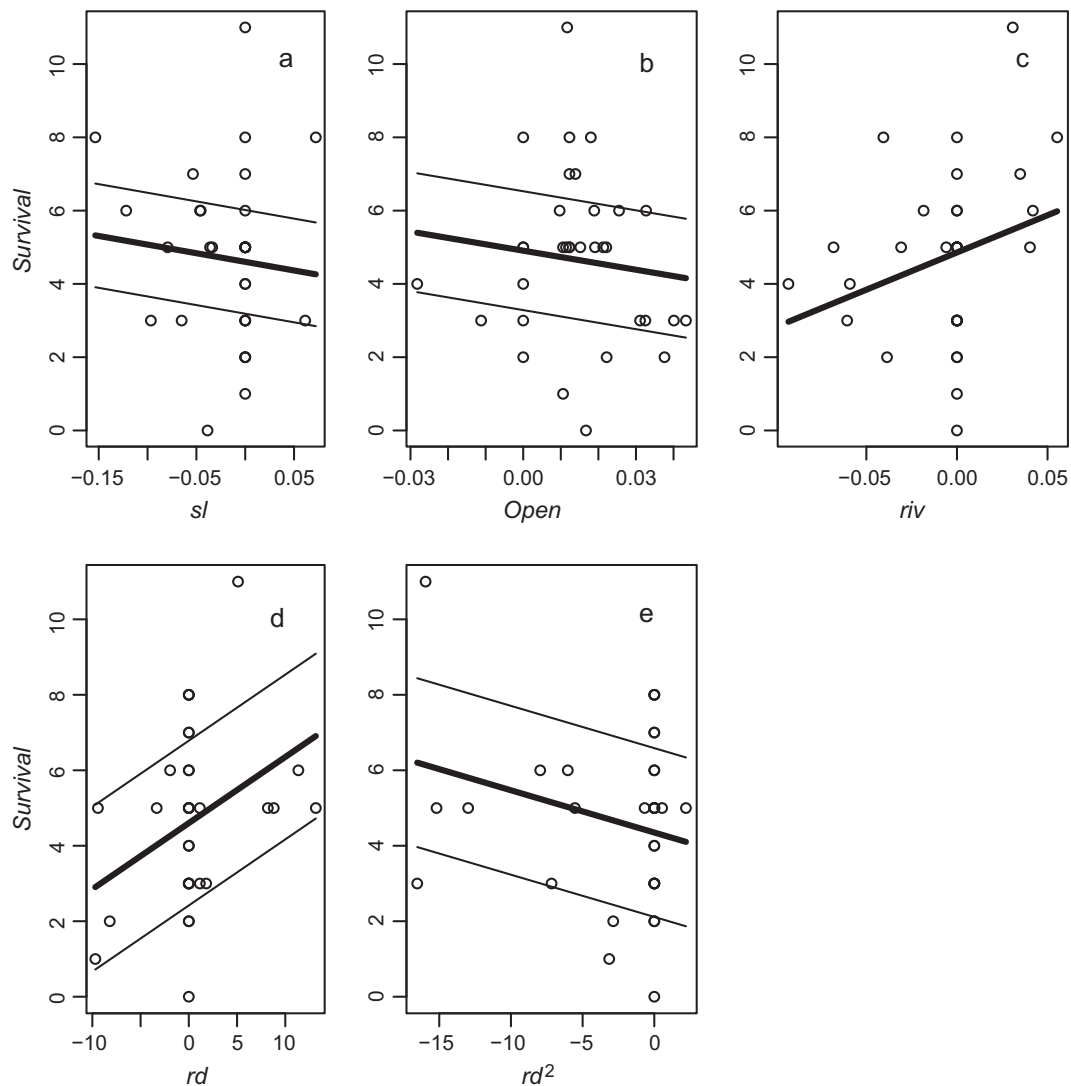
Fig. 2. Relationship between reproductive success (*y*-axis, measured as the number of pups survived to December 31, *survival*) and female wolf habitat selection (*x*-axes). The plots represent the results of the best-fit mixed-effect model M1 detailed in Table 2. The predictor variables in that model were regression coefficients derived from the resource selection functions detailed in Appendix S1: Table S1, and represent the strength of selection/avoidance in relation to slope (*sl*, panel a); openness (*open*, panel b); distance from rivers (*riv*, panel c); distance from roads (*rd*, panel d); and a squared term for distance from roads (*rd²*, panel e). For a detailed description of the predictor variables, see the *Methods* section and Table 1. The plots are based on mixed-effect models simplified by including only one predictor variable at the time. *Pack ID* was the random term in all models. The thick line denotes the predicted values for a "typical pack," while the thinner lines indicate the boundaries of the values predicted by 95% of the population of packs. The thinner lines are missing in panel (c) because the standard deviation of the random term in the *riv* model was close to 0, indicating very small variability among packs.

Of the regression models relating *prop* to the RSF coefficients, three had ΔAIC_c values <2 (Table 2). Collectively, these models indicate that *prop* was associated with habitat selection as it

pertains to slope and distance from roads (Table 2, Fig. 3).

Survival was not explained by interactions between fitness-related variables and habitat
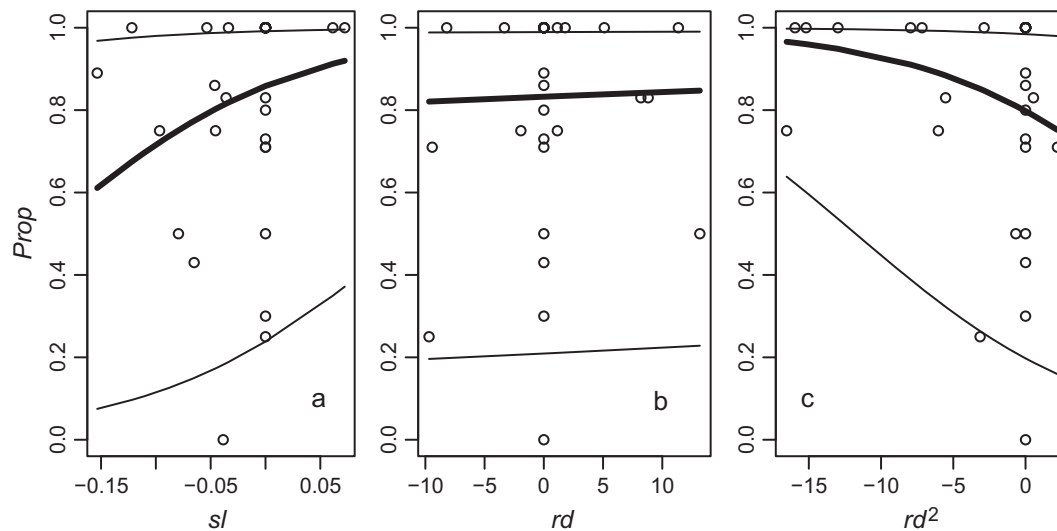
Fig. 3. Relationship between reproductive success (*y*-axis, measured as the proportion of pups survived to December 31, *prop*) and female wolf habitat selection (*x*-axes). The plots represent the results of the best-fit binomial mixed-effect models reported in Table 2. The predictor variables in that model were regression coefficients derived from the resource selection functions detailed in Appendix S1: Table S1, and represent the strength of selection/avoidance in relation to slope (*sl*, panel a); distance from roads (*rd*, panel b); and a squared term for distance from roads (*rd*^{2}, panel c). For a detailed description of the predictor variables, see the *Methods* section and Table 1. The plots are based on mixed-effect models simplified by including only one predictor variable at the time. *Pack ID* was the random term in all models. The thick line denotes the predicted values for a "typical pack," while the thinner lines indicate the boundaries of the values predicted by 95% of the population of packs.

selection. That is, none of the interactions between fitness-related variables and RSF coefficients were included in the final models. Or, if they were, their *P*-values were >0.05. However, for *prop*, we detected statistically significant interactions between some fitness-related variables and RSF coefficients. In particular, some variation in *prop* was explained by an interaction between habitat selection in terms of distance from roads and coat color (model A in Table 3), and pack size (models B1–4 in Table 3). Moreover, the relationship between *prop* and habitat selection based on slope was conditional on the abundance of conspecifics (models C1–4 in Table 3).

Discussion

In our study, we determined that not all habitat selection or avoidance behaviors performed by adult female wolves during the pup-rearing season were connected to their RS (Appendix S1: Table S1; Table 2). Selection of intermediate distances from roads and of open habitats and

avoidance of steep slopes were the only behaviors connected to RS. Moreover, the relationship between habitat selection and RS was further complicated by individual-, group-, and population-level factors (Table 3). Those habitat selection behaviors that were not devoted to benefit RS may be instead directed to benefit the other basic component of fitness, individual survival (Arlt and Pärt 2007), or overall fitness, that is, LRS. In some instances, habitat selection behaviors may even be an example of non-adaptive behavior (Kristan 2003, Robertson and Hutto 2006). Therefore, exploring the relationship between habitat selection and different components of fitness is vital in order to identify which habitats are essential for the success of the focus species and to determine to which purpose those habitats are selected.

Personality and culture are two additional aspects of habitat selection that are rarely explored in habitat selection studies (but see Boon et al. 2008). Habitat selection is a behavior and as such is influenced by many factors, including personality and culture (Kristan 2003, Robertson and Hutto

Table 3. Best-fit regression models (ΔAIC$_c$ < 2) predicting reproductive success from the interaction between habitat selection and several fitness-related variables.

M	gr	gr:rd	ps	ps:rd^2	ab	ab:sl	sl	rd	rd^2	df	logLik	AIC$_c$	ΔAIC$_c$
A	_1.4_	−0.3**							0.2*	5	−45.23	102.7	
B1							12.5*		−0.1*	4	−46.43	102.3	0.00
B2							15.8*	0.1	−0.2**	5	−45.73	103.7	1.39
B3			0.1	0.03			19.1*		−0.5*	6	−44.36	104.0	1.66
B4									−0.1*	3	−48.65	104.1	1.84
C1							12.5*		−0.1*	4	−46.43	102.3	0.00
C2							15.8*	0.1	−0.2**	5	−45.73	103.7	1.39
C3					−0.03	−1.7*	123.6*		−0.2**	6	−44.249	103.7	1.44
C4									−0.1*	3	−48.65	104.1	1.84

Notes: Reproductive success is expressed as the proportion of pups survived to the end of the year (_prop_). The fitness-related variables are coat color, including two categories: gray (_gr_) and black; abundance (_ab_), which is conspecific abundance in the study area; and pack size (_ps_), which is the size of the pack to which the female belongs. Abbreviations associated with habitat selection variables are defined in Table 1. The models are binomial regressions with _PackID_ included as a random-effect term. For details on candidate models and selection procedure, see the _Methods_ section. For each predictor variable, the table reports regression coefficients and significance levels, which are expressed as *$P \leq 0.05$ and **$P \leq 0.01$. M = model; df = degrees of freedom; logLik = log-likelihood; AIC$_c$ = Akaike Information Criterion corrected for small sample size; ΔAIC$_c$ = difference in AIC$_c$ compared to the best-fit model.

2006, Uboni et al. 2015_b_). Animals belonging to several taxa exhibit personality, which is the result of behavioral propensities that affect several aspects of the animal's behavior and that are different among individuals (Réale et al. 2007). Personality is particularly influential in determining RS (Dingemanse et al. 2004, Biro and Stamps 2008), and that could be partly the result of individual choices of habitat. Indeed, in our study system, habitat selection varied considerably among individuals (Appendix S1: Table S1). Moreover, the cultural footprint of each family group, that is, their culture, also seems to influence RS and habitat selection. In our study system, some packs experienced levels of RS consistently different from other packs (Fig. 4). Similarly, in the same study system, some packs tend to use their territory in a more conservative way than others (Uboni et al. 2015_b_). Additionally, Hebblewhite and Merrill (2008) assessed that wolves respond to human activities more consistently within packs than among packs.

We hypothesized that the strength of the relationship between habitat selection and RS in carnivores is intermediate compared to ungulates and birds—two taxa for which the relationship between RS and habitat selection has been studied. In ungulates, the habitat selected by a female when establishing its home range and during its daily movements is crucial to the survival of its calf (McLoughlin et al. 2006, 2007). In birds,

selection of a good nest site is most important to chick survival (Badyaev 1995, Aldridge and Boyce 2007, Sandercock et al. 2015), even though in some species adult habitat selection also plays a role in the survival of their offspring (Bloom et al. 2013). In carnivores, the habitat at the den is essential for pup/cub survival, but adult habitat selection is also important. Smith et al. (2015) observed that a significant proportion of intraspecific killing in YNP occurs during the denning period (March–May), when packs attack their neighbors at den sites. Moreover, carnivores usually select habitats far from human disturbances for their dens (Sazatornil et al. 2016), suggesting that the habitat at the den is crucial to ensure the wellbeing of their offspring. Nevertheless, adult habitat selection is also related to young survival (this study and Mosser et al. 2009, Rauset et al. 2015), likely because habitat selection determines hunting success—food availability for the young—and because the young start following the adults in their daily movements early in life. Thus, the habitat selected by the adults is important to protect the young from possible threats, such as adverse weather conditions, fatal accidents, and attacks of predators or competitors.

In our study system, selection of open areas was a predominant characteristic of habitat selection of female wolves during the pup-rearing
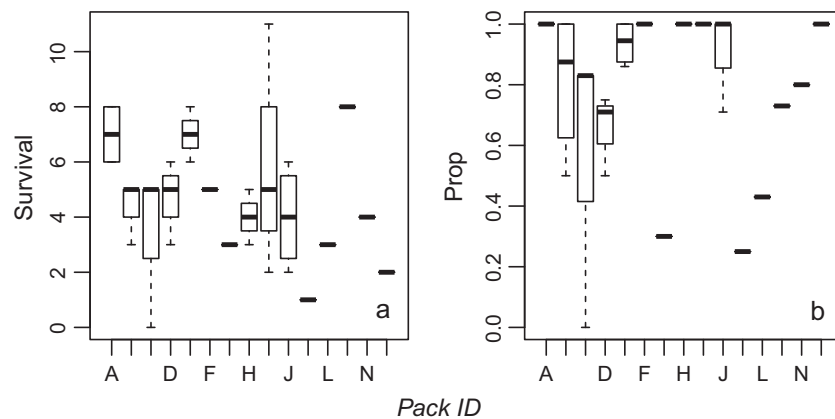
Fig. 4. Variability in wolf reproductive success (RS, *y*-axes) among 15 packs (*x*-axes, labeled with letters A–O) residing in Yellowstone National Park from 1997 to 2008. In panel (a), RS is reported as the number of pups survived to December 31 (*survival*), while in panel (b) as the proportion of pups survived to December 31 (*prop*). Data include 33 female/yr. The bold horizontal bars denote the median, the upper and lower edges of the boxes denote the interquartile range, and the dashed vertical lines extend to the range of data.

season. Twenty-five out of 33 female/yr (76%) positively selected open areas during the study period (Appendix S1: Table S1). Wolves are cursorial predators that travel long distances to find their prey. They often use natural or artificial corridors and open areas for traveling, detecting potential prey and successfully performing a kill (Kauffman et al. 2007, Courbin et al. 2013). Hence, selection of open areas may reflect wolf hunting behavior, which aims at maximizing prey encounter and hunting success (Kunkel and Pletscher 2001, Creel et al. 2005, Kauffman et al. 2007). However, selection of open areas was negatively correlated with RS (Table 2). Since intraspecific killing is a relevant cause of mortality among YNP wolves (Smith et al. 2015), we hypothesize that selection of open areas may cause wolf pups to be more vulnerable to conspecific attacks.

Avoidance of steep slopes and selection of intermediate distances from roads were the only habitat selection patterns explaining the variability in wolf RS measured both as *survival* and as *prop*. Avoidance of steep slopes may be related to the energetic costs incurred during traveling on such terrain, or to the risk of injury or fatality when hunting prey. Even though this is just a speculation, wolves' dislike for steep slopes is confirmed both by previous studies on wolf habitat selection (Hebblewhite and Merrill 2008, Houle et al. 2010, Milakovic et al. 2011, Whittington et al. 2011, Lesmerises et al. 2012, Uboni et al. 2015a) and by a

switch in elk preference toward steep slopes after wolf reintroduction in YNP (Mao et al. 2005). In YNP, wolf dens are often located near roads. In the park, wolves may not perceive roads as a threat, despite the heavy summer traffic, because of the absence of hunting and poaching (Uboni et al. 2015a). The vicinity of a road to the den site may benefit pup survival because roads are used as travel corridors and promote prey encounters (Kauffman et al. 2007, Courbin et al. 2013).

Lastly, habitat selection patterns related to distance from rivers explained some of the variability in RS measured as *survival* (Table 2). Wolf dens and rendezvous sites are usually located in proximity to watercourses (Joslin 1967, Matteson 1992, Thurston 2002, Ausband et al. 2010), suggesting that access to water is an important factor for wolf pup survival. Like roads, proximity to streams and rivers can facilitate prey encounter rates (Kunkel and Pletscher 2000, Kauffman et al. 2007). Additionally, access to water is important for a number of physiological needs for wolves, including digestion of protein-rich diets, thermoregulation during warm weather, and lactation for nursing females (Peterson and Ciucci 2003, Unger et al. 2009).

Despite the small sample size available for our habitat selection analysis (19 females followed over 12 yr, located once a week for most of the study period), we believe that our results are representative of the more general patterns of habitat selection exhibited by adult wolves in YNP, as our

results concur with previous studies on habitat selection of wolves in the same study area (Kauffman et al. 2007, Uboni et al. 2015*a*). Nevertheless, we suggest that GPS collars may be used instead of VHF collars for future research on this topic.

Habitat selection is the result of a complex combination of choices that an animal makes to ensure its own survival and fitness. Connecting habitat selection to a variety of measures of fitness is a useful way to disentangle the contribution of habitat selection to each component of fitness. Our results demonstrate that only a part of the choices made by an adult animal in terms of habitat selection are directed to increasing its RS. We recommend to include multiple measures of fitness in habitat selection studies in order to understand the mechanisms and motivations underlying habitat choices.

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