

EVIDENCE THAT ELEPHANTS, BEARS, AND SHEEP
CHOOSE HABITAT BY ASSESSING
ENVIRONMENTAL INFORMATION ACROSS
MULTIPLE SPATIAL SCALES

by

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A Dissertation submitted to the
Graduate School–Newark
Rutgers, The State University of New Jersey
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy
Graduate Program in Biological Sciences

Written under the direction of

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Newark, New Jersey

October, 2015

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ABSTRACT OF THE DISSERTATION

Evidence that elephants, bears and sheep choose habitat by assessing environmental information across multiple spatial scales

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Understanding the habitat preferences of large mammals is critical for their conservation and management. Resource selection functions (RSFs) can be used to assess these preferences, but they often only incorporate environmental information, such as percent tree cover, at a spatial resolution determined by the source of the data, i.e. satellite imagery. Organisms may respond to their surroundings at larger or smaller spatial scales, and thus the spatial scale of the data may be biologically irrelevant for the species in question. Instead, habitat selection should be assessed on a continuum of spatial scales to identify the ones that are most relevant to the organism. This can be accomplished by locally averaging, or smoothing, layers of environmental information to generate coarser representations of the organism's surroundings.

In Chapter 2, I model habitat preferences of savannah elephants with and without multiple spatial scales. Models that incorporated multiple spatial scales performed better

and made different predictions regarding the spatial distribution of high-quality habitat throughout a landscape. This chapter has been published in PeerJ (<https://peerj.com/articles/504/>).

The inclusion of multiple spatial scales for numerous environmental variables can lead to problems in model choice, as not all combinations of variables can be evaluated. In Chapter 3, I model habitat preferences of brown bears by first using the least absolute shrinkage and selection operator (lasso) to order the variables by their importance. I then fit models of increasing complexity by adding one variable at a time in reverse order of importance. I also incorporate the presence of neighboring individuals to account for the possible competitive exclusion of optimal habitat, but this was found not to affect the habitat chosen.

In Chapter 4, I determine whether individual desert bighorn sheep have different habitat preferences when they inhabit two mountain ranges with differing availability of freestanding water. For each environmental variable, both a full parameter and a ‘difference’ parameter are estimated, depending on where the sheep movement occurs. Different preferences were found for vegetation at multiple spatial scales, implying that bighorn sheep can utilize the moisture found within vegetation to survive when freestanding water is not available.

Acknowledgements

First and foremost, I would like to thank my friend and advisor, Gareth Russell, who has provided me with extensive knowledge, skills, and support throughout my graduate career. I am grateful for the opportunity I was given to work in his lab and to develop as an independent researcher.

I would also like to thank my committee members, Claus Holzapfel, Simon Garnier, and Julie Lockwood, for their thoughtful comments and suggestions. I am especially grateful to Grant Harris, who provided numerous contacts, data sets, and manuscript edits, as well as Stuart Pimm for his suggestions and edits.

The Russell lab was a large part of my success in graduate school. In addition to planning ecological-themed celebrations, they were always available to read and edit papers, work through coding issues, and chat about research. Thank you Jessica Schnell, Sarah Kornbluth, Tanya Lubansky, and Nidhi Dharithreesan. I am also grateful for the other students in my E&E cohort and will miss our frequent meetings to discuss journal articles and to edit papers.

I also thank my parents, Fran and Sharon, for always encouraging me to strive for excellence in everything I do. Lastly, I thank my wife and best friend, Kathi. She encouraged me to pursue my academic goals as we began to raise a family, and I will be forever grateful for her love and support.

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Chapter 1

Introduction

1.1 Habitat loss

Animals must consume resources to survive and reproduce. Resources are not often easy to acquire, so individuals must be selective when deciding where to obtain them (Manly et al. 2002). Habitats can be defined as the areas occupied by animals to acquire resources (Garshelis 2000). Some types of habitat may be preferred because they contain more resources for a particular species, while others might be avoided due to perceived negative qualities, such as the risk of predation (Rettie & Messier 2000). The use or nonuse of a habitat can therefore be linked to the quality of the habitat and the fitness it confers (Manly et al. 2002).

The global human population is growing at an exponential rate and consequently alters the environment in a multitude of ways (Roberts 2011). The conversion of the natural landscape for use in agriculture and construction is one of the leading causes of the degradation and fragmentation of habitat, which is the largest contributor to species endangerment and loss of biodiversity (Czech & Krausman 1997; Wilcove et al. 1998; Brooks et al. 1999; Chapin et al. 2000; Pimm & Raven 2000; Harcourt, Parks & Woodroffe 2001; Kerr & Deguise 2004). Habitat fragmentation reduces gene flow and can increase the extinction risk for wide-ranging species (Woodroffe & Ginsberg 1998; Tigas, Van Vuren & Sauvajot 2002; Coulon et al. 2004). In addition, urbanization and pollution can negatively affect ecosystem functioning and the quality of preferred habitats (Freedman 1995; Wilcove et al. 1998; Kerr & Deguise 2004; Lovett et al. 2009).

Human activity can also indirectly reduce available habitat (Walther et al. 2002). Global climate change is causing many plant and animal species to shift their geographic ranges to higher latitudes or altitudes (Easterling et al. 2000; Parmesan & Yohe 2003; Hickling et al. 2006; Chen et al. 2011). This shift can cause a spatial mismatch between animals and their resources if some species are not able to shift their ranges as well as others (Schweiger et al. 2008). Furthermore, organisms near the poles or in high altitudes are limited in their ability to shift their ranges due to shrinking habitat availability (Hickling et al. 2006). These anthropogenic impacts are the primary cause of the ongoing sixth mass extinction event (Wake & Vredenburg 2008; Barnosky et al. 2011).

1.2 Conservation of large mammals

Although many plant and animal species are threatened in the wake of these anthropogenic changes, large mammals are particularly prone to extinction (Cardillo 2003; Cardillo et al. 2005; Price & Gittleman 2007; Cardillo et al. 2008; Davidson et al. 2009; Macdonald et al. 2013). This is in large part due to the life history traits of species with large body size, such as lower reproductive rates and slower population growth, that lead to smaller population sizes (Purvis et al. 2000; Cardillo 2003; Cardillo et al. 2005; Sibly & Brown 2007; Bielby et al. 2007; Cardillo et al. 2008; Jones 2011; Macdonald et al. 2013). Larger organisms also need to consume more total resources than smaller organisms and thus often have large home ranges to meet their resource requirements (McNab 1963; Kelt & Van Vuren 2001; Macdonald et al. 2013). It has been observed that extinction risk is positively correlated with the range size of a species (Purvis et al. 2000; Price & Gittleman 2007; Cardillo et al. 2008). Large home ranges are more likely to overlap with those of conspecifics, leading to competition for resources (Burskirk

2004; Jetz et al. 2004). Additionally, habitat fragmentation has a larger effect on species with small population sizes (Henle et al. 2004) and large area requirements (Tigas et al. 2002), increasing extinction risk even further. Many large mammal species face the added risk of extinction through human hunting, either for food or for sport (Jerozolinski & Peres 2003; Johnson et al. 2010; Macdonald et al. 2013). However, sustainable hunting has been used as a tool for the conservation of valuable species, such as white rhinos (Leader-Williams et al. 2005).

The successful conservation of large mammals is important for several reasons. Many carnivorous large mammal species can affect the structure of their entire ecosystem by controlling the population sizes of herbivores (Estes et al. 1998; Berger et al. 2001; Estes et al. 2011). Their loss can thus indirectly reduce plant biomass (Berger et al. 2001), increase soil nitrogen mineralization (Frank 2008; Estes et al. 2011), and transform forests into grasslands through tree recruitment failure (Beschta & Ripple 2009; Estes et al. 2011). For example, when gray wolves (*Canis lupis*) and grizzly bears (*Ursus arctos*) were extirpated from the southern Greater Yellowstone ecosystem, the moose (*Alces alces*) population grew rapidly, which caused a decrease in the height and density of local willow (*Salix* spp.) trees (Berger et al. 2001). This in turn reduced the diversity and density of the riparian avian community (Berger et al. 2001).

These top-down trophic effects are widespread (Schmitz, Hamback & Beckerman 2000), and reintroduction of top predators does not always restore the environment (Wolf, Cooper & Hobbs 2007). In Yellowstone National Park, beavers (*Castor canadensis*) use willow for food and building material for their dams, which in turn alters the structure of the riparian areas to be suitable for willow establishment (Bigler, Butler

& Dixon 2001; Baker & Hill 2003; Westbrook, Cooper & Baker 2006). When wolves were extirpated, willow herbivory by elk (*Cervus elephus*) intensified, thus reducing this resource for beavers and ultimately the beaver population (Beschta & Ripple 2006). Wolf reintroduction was expected to positively affect willow populations by reducing browsing by elk, but the change in structure caused by the reduction of the beaver population and their dams precluded the recovery of willow (Singer, Mark & Cates 1994; Wolf, Cooper & Hobbs 2007).

Large herbivores can alter the vegetation structure of the community, which can affect biodiversity and population sizes of other organisms (Rutina, Moe & Swenson 2005; de Beer et al. 2006; Valeix et al. 2011). Elephants act as ecosystem engineers by uprooting trees and large bushes, changing both food availability and visibility (Valeix et al. 2011). This may facilitate other smaller herbivores by stimulating higher growth rates in heavily browsed plants and providing better visibility to detect approaching predators (Fornara & Du Toit 2007; Valeix et al. 2011).

Despite these benefits of large mammals, there are also many instances of conflict between humans and wildlife. Some examples include the destruction of crops, water sources, and property by elephants (Hoare 2000; Graham et al. 2010; Baskaran et al. 2010; Gubbi et al. 2014); predation of livestock by wolves, leopards, and other large carnivores (Schiess-Meier et al. 2007; Zarco-Gonzalez, Monroy-Vilchis & Alaniz 2013; Caniglia et al. 2013); the raiding of anthropogenic garbage and disturbance of hikers by bears (Schirokauer & Boyd 1998; Greenleaf et al. 2009); and injury and death to humans (Herrero et al. 2011; Liu et al. 2011; Can et al. 2014). This can lead to lethal responses by affected communities and a general lack of sympathy for the offending species (Liu et al.

2011; Mijeles et al. 2013; Kinsky & Knight 2014; Can et al. 2015; Gubbi et al. 2014). Successful conservation of these populations hinges on the ability to adequately protect human interests as well.

Managers and conservationists must be able to accurately identify and predict species' habitat requirements in order to successfully protect and conserve them. To this end, models of habitat selection have been developed and fine-tuned to aid in protecting the appropriate habitat for a particular species.

1.3 Modeling habitat selection

Models of habitat selection compare the locations of individuals in a population or species of interest with potentially important environmental variables. Locations of individually identified organisms may be obtained using radio or satellite telemetry (Aarts et al. 2008), leg bands (Robinson et al. 2010), or unique markings on individuals (Lubansky 2015). Environmental information is often either measured directly in the field (e.g., Anderson et al. 2005) or derived from satellite imagery (Gottschalk, Huettmann & Ehlers 2005). This information is stored as a raster layer and can represent vegetation, distance to point objects, or terrain features. Vegetation layers can either be categorical, where each resource unit is a particular habitat type, or continuous, where each resource unit is the proportion of the habitat types found within the unit. Distance from fixed features such as bodies of water or roads are created using GIS. Digital elevation models (DEMs) provide information on elevation and can be used to derive other measurements such as slope and ruggedness.

When a particular resource unit is used more frequently than would be expected given its availability, selection for that resource is inferred (Johnson 1980; Manly et al.

2002). This selection can be quantified using a resource selection function (RSF), where the values of the resource units are proportional to their probability of use (Manly et al. 2002). There are two primary designs when developing an RSF: the used/unused design, where each resource unit is classified according to whether an organism was observed there or not; and the use/availability design, where a sample of used resource units are compared to a sample of available resource units (Garshelis 2000; Manly et al. 2002). One problem with the used/unused design is that while used locations are known with certainty, it is difficult to determine if a location is truly unused or if an individual was simply not detected (Keating & Cherry 2004; MacKenzie & Royle 2005; Johnson et al. 2006; Duchesne et al. 2010). Mistakenly including locations that were actually used can bias parameter estimates and reduce the model's ability to detect selection (Gu & Swihart 2004; MacKenzie & Royle 2005). Under a use/availability design, available locations may include both used and unused locations (Keating and Cherry 2004), but this does not affect the estimation of the parameter coefficients unless the proportion of used locations is high (Nielson, Manly & McDonald 2003; Johnson et al. 2006).

In the standard design, used resource units are taken from all animals under study and compared to available resource units sampled from the entirety of the study area. The resulting RSF is often analyzed using logistic regression, particularly if the habitat variables are continuous (Thomas & Taylor 2006). However, individuals may not be able to reach all areas of their home ranges within the interval between fixes if the interval is small (Arthur et al. 1996). To account for differing availability of habitat for each individual or across different parts of an individual's home range, a matched use/availability design may be used (McLoughlin et al. 2010). Under this design, each

used resource unit is matched to a set of randomly chosen available resource units drawn from a circle around the used unit, usually equal to the distance an individual can travel between location fixes (Arthur et al. 1996; Cooper & Millsbaugh 1999; Hjermann 2000; Boyce et al. 2003; Boyce 2006; Duchesne et al. 2010). This RSF can be analyzed using conditional logistic regression, which evaluates the likelihood of a pair of locations as an independent movement (Fortin et al. 2005; Fortin et al. 2009; Duchesne 2010). Even within a small radius, the availability of a particular resource unit is dependent upon its distance from the individual's current location (Hjermann 2000). When the habitat quality is relatively equal, individuals are more likely to choose locations that minimize travel costs – the time and energy that it takes to move from one location to another (Harris et al. 2008). Hjermann (2000) introduced a continuous availability function where availability decreased as a function of distance from the individual's current location. Another approach is to explicitly include a coefficient for the distance between the current location and each potential destination (Forester, Im & Rathouz 2009). Failure to incorporate the travel cost can yield biased estimates of parameter coefficients (Forester, Im & Rathouz 2009).

Every available location within the radius of movement choices can be described by a list of potentially important values that correspond to the environmental features at that location, such as percent forest cover or elevation. Conditional logistic regression calculates the probability of choosing a particular location relative to other available locations. Under this model, the relationship between the movement and the environmental features is described by a list of unknown parameters to be estimated. For each movement, the chosen location is assigned a value of 1, and the non-chosen

locations are assigned a value of 0 (McLoughlin, Coulson & Clutton-Brock 2008). The probability p_j is only evaluated for chosen locations using the following equation:

$$p_j = \frac{e^{x_j\beta}}{\sum_j e^{x_j\beta}}$$

where \mathbf{x}_j is the list of environmental values and β is the list of unknown parameters that describe the relationship between the movement and the environmental variables. Thus $e^{x_j\beta}$ for the chosen location (where $y_j = 1$) is divided by the sum of $e^{x_j\beta}$ for every available location. The log-likelihood of a single movement L_i is the logarithm of p_j , and the log-likelihood of the entire movement dataset is the sum of L_i over every movement i . The unknown parameters β are estimated after fitting the model using non-linear maximization of the log-likelihood. This process is repeated for different combinations of environmental variables, and the resulting log-likelihoods are compared using information-theoretic approaches such as Akaike's Information Criterion (AIC; Anderson & Burnham 2002; Burnham & Anderson 2002). As more variables are added to a model, the fit of the model improves. However, models that are too complex are limited in their predictive ability. AIC is a measure of parsimony, or the balance between fit and complexity. Every variable added to a model is assessed a penalty term; therefore, the improvement in fit must be large enough to justify the additional complexity. The model with the combination of variables that produces the most parsimonious AIC score is thus chosen (Hirzel & Le Lay 2008).

The environmental data used to evaluate habitat selection are usually at a spatial scale determined by the source of the data (i.e., satellite imagery). However, organisms may respond to their environment at smaller or larger scales, depending on spatial context

or the perceptual ability of the organism (Holling 1992; Lima & Zollner 1996; Nams 2005; De Knecht et al. 2010; Marshall et al. 2011). This scale may even be biologically irrelevant to the species in question, limiting model inference and producing misleading results (Levin 1992; Boyce 2006; Mayor et al. 2009; Wheatley & Johnson 2009; De Knecht et al. 2011). Therefore, habitat preferences should be evaluated on a continuum of scales to determine the ones to which an organism is responding (Fisher et al. 2011).

Preferred habitat is often assumed to correlate with high-quality habitat, but it more accurately has a higher *probability* of being high-quality habitat (Mathewson & Morrison 2015). Habitat quality is defined by its ability to provide resources for an individual's survival and reproduction and can only be assessed by measuring the demographics of individuals or populations (Garshelis 2000; Railsback, Stauffer & Harvey 2003; Johnson 2007; Morrison 2009). Therefore, measures of an area such as population density or habitat use may be misleading if that area does not confer a higher fitness to the individuals that are found there (Mosser et al. 2009; Mathewson & Morrison 2015). Habitat that does not confer high fitness may be used by organisms for a variety of reasons. Individuals may be forced to occupy sub-optimal habitat due to competitive exclusion or to avoid predators (Mosser et al. 2009; McLoughlin et al. 2010). Habitat quality may also change from year to year due to differences in rainfall. Identifying preferred habitat can still provide important information regarding the most likely movement choices of individuals, but when managers make decisions regarding habitat restoration or population management, this information should not be used without carefully considering how the available resources within these habitats will affect the survival and reproduction of the population.

1.4 Objectives

Habitat selection by animals is a complex process. Despite the improvements made to modeling techniques, many challenges remain to accurately identifying preferred habitat. The primary objective of this dissertation research was to improve upon models of habitat selection of large mammals. This was accomplished by: (1) explicitly incorporating spatial scale into RSFs; (2) determining habitat preferences in the presence of conspecifics; (3) resolving the issue of too many predictor variables in complex landscapes; (4) using unclassified spectral characteristics to represent vegetation in habitat selection models in a desert environment; and (5) modeling differences in habitat preferences between individuals moving between two separate locations through the use of 'difference' parameters.

Objective (1) was completed using location data of savannah elephants found in two parks in southern Africa: Etosha National Park and Maputo Elephant Reserve. Conservation efforts have led to an increase in the number of individual elephants inhabiting the parks, but a high population density can lead to ecosystem degradation and reduced biodiversity (Owen-Smith 1996; Whyte, Van Aarde & Pimm 2003; Guldmond & Van Aarde 2007; Van Aarde & Jackson 2007; Harris et al. 2008). One solution to this problem is to provide elephants with more space (Harris et al. 2008). This is contingent on the ability to accurately project preferences to other parts of a landscape to predict where elephants are likely to go. Because individuals may have different preferences for the same habitat at different scales, extrapolating local preferences can result in misleading predictions. For example, elephants may have a fondness for individual trees, but an extrapolation of this preference across the landscape would indicate that large

contiguous forests are ideal, which may not be the case. We included environmental information at multiple spatial scales to account for differing preferences and to improve projections of landscape-wide habitat quality. This study has been published in PeerJ (<https://peerj.com/articles/504/>).

Objectives (2) and (3) were completed using location data of brown bears from the Kenai Peninsula, Alaska. This population has declined in recent years in part because of increasing human activity on the Peninsula (Suring & Del Frate 2002; Goldstein et al. 2010). Identifying preferred areas is thus important to minimize human-bear conflict. Unlike elephants, however, brown bears do not travel in groups across large areas of the landscape, but instead occupy small areas with little overlap with conspecifics. Consequently, some individuals might be restricted in their choice of available habitat by neighboring bears (Thomas & Taylor 2006). In addition, the Kenai Peninsula is very heterogeneous and requires a large number of environmental variables to represent the available habitat. Therefore, the incorporation of multiple spatial scales created too many predictors to be evaluated using standard model selection via AIC. We instead used the least absolute shrinkage and selection operator (lasso) to generate a ranking of important predictors that were used to inform model selection.

Objectives (4) and (5) were completed using location data of desert bighorn sheep in Joshua Tree National Park, California. Individual sheep had been tagged within a single mountain range to study their use of water guzzlers located on the mountain (Longshore et al. 2009). It was observed that two individuals frequently traveled to a nearby secondary mountain range that lacked any documented permanent water. Bighorn sheep have been shown to require freestanding water for their survival (Blong & Pollard

1968; Turner 1970; Broyles 1995; Turner et al. 2004; Oehler et al. 2005; Dolan 2006; Sappington et al. 2007; Wehausen 2007; Longshore et al. 2009; Bleich et al. 2010), but other studies have indicated that individuals can obtain enough moisture from plant succulence alone (Warrick & Krausman 1989; Krausman & Etchberger 1995; Broyles & Cutler 1999). Vegetation is thus an important component of sheep habitat, but maps of vegetation in desert environments are difficult to create because of the scarcity of vegetation and dominance of soil reflectance (Smith et al. 1990). As an alternative, we used unclassified spectral imagery to represent the moisture content of the vegetation and soil. We hypothesized that individual sheep are able to cross the valley into the secondary mountain range because of an increased availability of this variable. To model whether these individuals have different habitat preferences within the different mountain ranges, we estimated two sets of parameters for each predictor variable, depending on where the movement took place: the primary parameter was estimated using all movements by a group of sheep, whereas the “difference” parameter was estimated using only sheep movements in the secondary mountain range. If individuals do have different preferences within the different mountain ranges, the inclusion of this difference parameter will result in a better prediction of sheep movements.

Chapter 2

Data-driven discovery of the spatial scales of habitat choice by elephants

2.1 Summary

Setting conservation goals and management objectives relies on understanding animal habitat preferences. Models that predict preferences combine location data from tracked animals with environment information, usually at a spatial resolution determined by the available data. This resolution may be biologically irrelevant for the species in question. Individuals likely integrate environmental characteristics over varying distances when evaluating their surroundings; we call this the scale of selection. Even a single characteristic might be viewed differently at different scales; for example, a preference for sheltering under trees does not necessarily imply a fondness for continuous forest. Multi-scale preference is likely to be particularly evident for animals that occupy coarsely heterogeneous landscapes like savannahs. We designed a method to identify scales at which species respond to resources and used these scales to build preference models. We represented different scales of selection by locally averaging, or smoothing, the environmental data using kernels of increasing radii. First, we examined each environmental variable separately across a spectrum of selection scales and found peaks of fit. These ‘candidate’ scales then determined the environmental data layers entering a multivariable conditional logistic model. We used model selection via AIC to determine the important predictors out of this set. We demonstrate this method using savannah elephants (*Loxodonta africana*) inhabiting two parks in southern Africa. The multi-scale

models were more parsimonious than models using environmental data at only the source resolution. Maps describing habitat preferences also improved when multiple scales were included, as elephants were more often in places predicted to have high neighborhood quality. We conclude that elephants select habitat based on environmental qualities at multiple scales. For them, and likely many other species, biologists should include multiple scales in models of habitat selection. Species environmental preferences and their geospatial projections will be more accurately represented, improving management decisions and conservation planning.

2.2 Introduction

Successful species conservation and management requires understanding the resources needed for their reproduction and survival (see Roever, Van Aarde & Leggett, 2012; Roever et al. 2013; Roever, Van Aarde & Chase, 2013). Because some resources are difficult to identify directly, habitat preferences can serve as proxies (Young, Ferreira & Van Aarde 2009). They, in turn, are revealed by the locations and movements of individuals within their landscape (Manly et al. 2002; Aarts et al. 2008; McLoughlin et al. 2010; Fisher, Anholt & Volpe, 2011; Roever et al. 2013). Models of habitat preference usually incorporate raster-based information, such as vegetation maps, at a spatial resolution determined by the data source (e.g., satellite imagery). This practice assumes that animals judge habitats at the same level of detail, or *scale*. However, organisms may respond to more fine-grained variation, or coarser, aggregated qualities, depending on the spatial context or their perceptual ability (Holling 1992; Lima & Zollner 1996; Nams 2005; De Knegt et al. 2010; Marshal et al. 2011). In fact, the resolution of the data may

be biologically irrelevant for the species in question, which can limit model inference and produce potentially misleading results (Levin 1992; Boyce 2006; Mayor et al. 2009; Wheatley & Johnson 2009; De Knecht et al. 2011).

A priori, biologists rarely know the spatial scale at which species select resources. Further, there is evidence that for some organisms, a single “characteristic” scale (Holland, Bert & Fahrig 2004; De Knecht et al. 2010) may inadequately characterize an environmental response (Mayor et al. 2009; Wheatley & Johnson 2009; Fisher, Anholt & Volpe 2011; Shrader et al. 2012). Here, we demonstrate how to identify the most important scale(s) of habitat selection by examining relationships between species movements and environmental attributes over a continuum of scales. We show that this data-driven approach changes the predictions of the amount and distribution of suitable areas across the landscape.

For a human example of multiple preference scales, imagine a suburban family that enjoys shopping. In the suburbs, stores are aggregated in a characteristic way, with high local concentrations (plazas, malls, etc.) separated by areas with few or no stores. Most of the area in Fig. 2.1a, in which dark grid squares represent high store density, has the suburban pattern. The path of the family’s travels – the black line – clearly shows that shopping areas are frequent targets. An analysis focusing only on the suburbs would reveal a preference for high store density.

Next, consider the area in the lower right corner. Knowing only store data, we would rightly guess that this is a city. A naïve extrapolation of the family’s suburban movements would predict frequent visits to this city, where stores are abundant. However, we would be completely wrong; our hypothetical family avoids cities. They do

so because despite attractive qualities, such as high store density, cities have perceived disadvantages: crowds, lack of parking, and so on. These attributes only become important when store density is assessed at a larger scale than that of a suburban mall. The key point is that the data describing store density serves as a proxy for different qualities at different scales. To unravel this, we can locally average, or smooth, these data with an increasingly larger radius. Fig. 2.1b shows the store data smoothed using a 21-pixel Gaussian filter. This converts the landscape to a map of *large-scale* urban density, and we can interpret the family's travels as "avoiding the city." By including both the original density map and the smoothed version in a model, we simultaneously discover the preference for isolated stores and the avoidance of large aggregations of stores. Even if we did not know exactly why this family avoids high store densities, our predictions of their future travels will be more accurate.

A previous study on savannah elephants from Maputo Elephant Reserve, Mozambique and Etosha National Park, Namibia, incorporated travel costs with other habitat variables to generate landscape-wide quality maps (Harris et al. 2008). They determined habitat preferences using variables at a 500 m resolution, which is very detailed given that elephants can move across thousands of square kilometers within a year. These models were able to accurately predict local movement choices, that is, the places that elephants chose over their immediate neighbors in the areas where they had been observed. However, their ability to provide regional predictions might break down when extrapolated over a broader landscape, such as the entirety of a reserve (see also Roeber, Van Aarde & Legget 2013). By analogy to the store example, elephants in more open savannah might tend to stay near trees while avoiding large forests.

Using the same dataset as the earlier study, we tease apart these *scale-dependent preferences* by smoothing each of the original environmental variables at different radii and assessing how well each explains animal movements. (Operationally, we define “scale” as the width of the radius used to smooth the original environmental data, so scale 0 refers to the original data). All of the variables, each at one or more identified optimal scales, are then used in a model selection process to generate a final landscape preference model. While our multi-scale models agree with the previous findings that elephants prefer to occupy areas that are near water, have high vegetation cover, and are far from human settlement, they predict local movements much better than models that use only a single scale. The multi-scale models can also produce very different predictions of landscape-wide habitat quality, potentially improving conservation directives that aim to protect essential habitats.

2.3 Methods

2.3.1 Study sites

Maputo Elephant Reserve and the Futi River corridor, which extends south of Maputo and is also included in the analysis, are located in the subtropical savannahs of southern Mozambique. At the time of the study, the reserve (*c.* 800 km²) was unfenced except for a 30 km stretch in the northwest (Harris et al. 2008). At least 311 elephants lived in the reserve and the corridor when these data were collected (Olivier, Ferreira & Van Aarde 2009). Etosha National Park (*c.* 23,000 km²) is located in the arid north-central part of Namibia. This park was fenced and held approximately 2,000 elephants at the time of the study (Etosha Ecological Institute, unpublished data).

2.3.2 Location data

GPS collars provided elephant location data (held by CERU, www.ceru.up.ac.za/). In Maputo they provided fixes every two to five hours, with collars active for 24 hours and off for 48 hours (Harris et al. 2008). Three males and two females wore collars covering the wet seasons (November-March) of 2000 and 2001 and the dry seasons (April-October) of 2001 and 2002. In Etosha, location data from six females were taken every eight hours and encompassed the wet seasons of 2002 and 2003 and the dry season of 2003 (Harris et al. 2008). Each female that was collared represented the movements of an entire herd. The data collection was facilitated through permission from the Namibian Ministry of the Environment (Research Permit number 580).

Individual movement patterns and habitat selection vary with sex (Stokke & Du Toit 2000; Woolley et al. 2009) and season (Wittemyer et al. 2007; Young, Ferreira & Van Aarde 2009; Young & Van Aarde 2010). Therefore, we combined location data in each reserve separately for males and females during the wet and dry seasons. Analyses were seasonal in resolution, so we did not partition movements by time of day. This yielded four data sets for Maputo and two for Etosha (for which only females carried collars). A pair of x, y coordinates represented the starting and ending location of each movement. We considered only those movements within a choice radius of < 5 km, because fast, long-distance movements may carry a different signal of habitat selection than slower, shorter movements (Morales et al. 2004; Roever et al. 2013). This process retained $> 80\%$ of the movements in each dataset.

2.3.3 Landscape data

The landscape variables consisted of vegetation, distance to water, and distance to human settlement. In Maputo, vegetation data included the proportion of reeds and tree cover. In Etosha, the vegetation variables included the proportion of mopane, *Acacia nebrownii*, and *Acacia*-dominated savannah (henceforth, *Acacia*). All raster-based variables had a cell, or pixel size, of 500 m by 500 m. We standardized each variable to have zero mean and unit standard deviation across the entire landscape.

We created squared versions of each variable and included these in the smoothing and model selection process where appropriate (see below). This allows for a variety of non-linear preference functions, including those in which an intermediate level of a variable is preferred (Johnson, Seip & Boyce 2004; Johnson & Gillingham 2005). This possibility is likely to be important if animals integrate their surroundings. For example, imagine an animal that likes open spaces in a savannah habitat, a mosaic of trees and grassland. At the fine scale, it might show a monotonic preference for open space, but at a larger scale, it would prefer the intermediate level of tree cover that characterizes a savannah. Expanding on this example, Fig. 2.2 describes possible interpretations of different combinations of preference function shapes at different scales.

2.3.4 Smoothed landscape data

We created smoothed vegetation variables by averaging each pixel with its neighbors within increasing radii up to 20 pixels, i.e., 10 km (Fig. 2.3). The functional form of the smoothing kernel should approximate the way an individual integrates its surroundings. For example, a flat smoothing kernel, where all pixels are weighted equally within a given radius, would be appropriate if an individual's ability to assess information

remained constant within that radius, and then dropped off dramatically (e.g. Holland, Bert & Fahrig 2004; De Knecht et al. 2011). Equally plausibly, an individual's perceptual abilities might decline gradually with distance. This could be caused by any number of mechanisms, such as diffusion and decay of chemical signals or progressive visual obstruction by vegetation. To account for this range of possibilities we included a linear decay parameter d , which affects the weight given to each pixel in the average depending on its distance from the central pixel. For the flat kernel, $d = 0$ (Fig. 2.4a). We allowed d to increase in steps of 0.1 (Fig. 2.4b) up to a maximum of $d = 1$, where the smoothing kernel declines linearly to 0 at the edge of the radius (Fig. 2.4c). This parameter was optimized along with the radius (see below).

We did not smooth 'distance to' variables because they are intrinsically smooth. We did create a squared version of 'distance to water' along with a squared version for each vegetation variable at each scale.

When smoothing, we can treat landscape values outside the spatial extent of the available data in one of two ways: either as true zeroes that represent habitat unsuitable for the organism (e.g., an ocean for a terrestrial mammal), or as unknown values. There may also be physical boundaries, such as fences, within the areas under consideration. In the case of a fence, while an animal may be unable to visit a location outside the fence, it is unclear whether it will take into account the bordering habitat when choosing a location inside the fence. In our study, fences coincided with the border of our landscape data in parts of Maputo and all of Etosha. While we may not know the habitat immediately bordering the reserve, there is no reason to think it is radically different from

what is inside. We therefore smoothed using the average of only those pixels within the smoothing radius that are also within each reserve, generating a ‘neutral’ boundary.

2.3.5 Habitat selection model

Resource selection functions (RSFs) specify the probability that a particular resource (or in this case, habitat) is chosen by an animal (Manly et al. 2002). These functions have been increasingly used to assess habitat selection based on movement data (i.e. McLoughlin et al. 2010), especially for elephants (Roever, Van Aarde & Legget 2012; Roever et al. 2013; Roever, Van Aarde & Chase 2013; Roever, Van Aarde & Legget 2013). For input they require a set of movement data and a set of landscape variables (or ‘layers’) describing the environment in which the organism(s) are moving.

Except for the most mobile animals, not all habitats can be reached in a given time interval, such as the 8 hour GPS fix interval. Therefore, only a subset of habitats within a certain radius of an individual are even candidates for being ‘chosen’ (Arthur et al. 1996). For any given movement i , each potential destination pixel j has a vector of k potential predictor values \mathbf{x}_j , derived from the landscape raster layers. Included in these values is a distance term between the current location and each potential destination pixel, which represents the cost of movement (Hjermann 2000; Harris et al. 2008). The actual choice \mathbf{y}_j is represented as a binary response, where the chosen location is given a value of 1 and all other locations, or a random subset of them if there are too many, are given a value of 0. Thus, the complete dataset for a single movement consists of a matrix \mathbf{X}_i and a binary column vector \mathbf{y}_i , in our case covering the chosen destination pixel and 29 random alternative destinations in a 10-pixel circular neighborhood of the starting pixel.

Under the conditional logistic model, the probability p_j that an animal will choose a pixel j as its next location is

$$p_j = \frac{e^{x_j\beta}}{\sum_j e^{x_j\beta}}$$

where β is a k by 1 vector of parameters to be estimated. L_i , the log-likelihood of a particular movement, is simply the logarithm of the value of p_j for the chosen destination pixel (the case where $y_j = 1$). The log-likelihood of the entire data set is the sum of the L_i over all movements i . We fit the model using non-linear maximization of log-likelihood using a quasi-Newton method implemented in the *Mathematica* software package (Wolfram Research 2012), and compared the models' performance using Akaike's Information Criterion (AIC).

Harris et al. (2008) found that the estimated model parameter applying to the 'travel distance' variable was extremely consistent across elephants and varied very little with the inclusion of other landscape variables. We followed their suggestion by first fitting that term separately and then using the fitted value as a fixed term when optimizing the other parameters.

2.3.6 Choosing optimal smoothing scales

There are two steps in the model discovery process. The first is the identification of candidate smoothing scales for each variable. The second is the inclusion of all the candidate variables (original or smoothed) in a model selection process.

To identify candidate scales, we smoothed each variable independently within increasingly larger radii. The radius extended from 0 pixels (the original data) to a maximum of 20 neighboring pixels (10 km), which is twice the radius of the local

neighborhood of movement choices. (In initial runs we encountered an issue with over-smoothing if the radius was too large, which produced unusual results; see Discussion.) At each radius we fit three models: one that included only the distance from current location, one with distance and the smoothed variable, and one that also included the smoothed variable squared. In each case we recorded the AIC score, generating three lines of AIC values (one of which, for distance only, is a constant). Candidate scales were chosen by looking for minima in the AIC lines. (In the figures, we invert the AIC axis so that the best models are peaks.) After identifying the candidate scales, we then optimized the decay parameter for each scale.

An alternate approach would be to smooth all landscape variables together at the same scales, instead of independently (Fisher, Anholt & Volpe 2011). This would be appropriate if, for example, a single constraint determined the manner in which organisms integrate their environment, such as their perceptual ability or physiology, which applied equally to all variables (Lima & Zollner 1996). We tested this but found that after the final model selection process (see below), the ‘separate scales’ model always equaled or outperformed the ‘same scales’ model, so we did not continue this analysis. The reason seems to be that when we smooth all variables together, the smoothing profile will typically be dominated by the variable that has most impact on the likelihood values. The best scales for the other variables remain hidden.

2.3.7 Choosing the final model

After identifying the candidate smoothing scales for each variable, we entered the linear and/or quadratic versions of these variables, distance from current location, distance from water, distance from human settlement (if applicable), and any original variables that had

optimal AIC scores into a model selection process. We used AIC to determine the most parsimonious model, and to create a parameter-averaged model based on AIC weights (Burnham & Anderson 2002). For comparison (see below), we repeated the model selection process, only allowing ‘base’ (original, non-smoothed) variables (as per Harris et al. 2008).

2.3.8 Two kinds of predictions

We created two types of habitat quality maps using the parameter-averaged model. The first type of map has quality values given by p_j , which measure relative *local* quality. Since this is the basis for the conditional logistic model, these maps illustrate model fit. We only show the predictions for the neighborhoods surrounding the start of each observed movement. Each map was then overlaid with movement *end*-points to show how well these coincide with predictions of locally optimal locations.

We also calculated the mean deviation of the probability value of each chosen pixel from all other pixels in its local 10-pixel neighborhood. Large positive values indicate that a high-quality pixel (preferred habitat based on model prediction) was chosen out of a variety of options, large negative values indicate that a low-quality pixel was chosen, and intermediate values mean either that a medium-quality pixel was chosen, or that there was very little variation (the landscape was relatively uniform). To assess the impact of including multiple scales of preference, we created local prediction maps and calculated mean deviations for the base-scale models and compared them to the multi-scale models using histograms.

The second type of map has quality values given by $e^{x_j\beta}$, a measure of relative *landscape-wide* quality. These values were calculated for the entire landscape (an

extrapolation). As above, each map was overlaid with movement end-points, this time to assess how well they predict the landscape-wide distribution of the elephants. Equivalent maps that do not allow smoothed variables were also created for comparison. Fig. 2.5 shows the complete process for one dataset: male elephants in Maputo during the dry season.

2.4 Results

2.4.1 Multiple scales and model performance

For all elephant groups at both reserves, model fit peaked at distinct smoothing radii (scales) for different habitat variables when considered individually. In many cases, a variable showed multiple peaks at different scales (Fig. 2.6; Table 2.1). After multivariate model selection using these scales, in each of our six datasets, the best multi-scale model was more parsimonious than the corresponding best base-scale model, according to AIC (Table 2.2). The difference in AIC score for Maputo datasets ranged from 31.0 to 48.5. In Etosha, the dry season models differed by 15.6, the smallest difference between any two models; this is evident in the similarities of the landscape-wide preference maps (see Fig. 2.8). The difference between the wet season models is 68.9; this also corresponds to the most striking difference between the preference maps (see Fig. 2.8). Overall, the results indicate that these elephants are using aggregated habitat attributes when deciding where to move, but in a different way depending on the season, the reserve, and the sex of the elephants.

2.4.2 The shapes of the relationships

Each elephant group displayed a quadratic preference relationship with at least one

Maputo Females, Dry Season

Variable	Decay	Best model parameter value	Importance	Parameter- averaged value
Distance	-	-1.10	1.00	-1.10
Reeds 4	0.0	0.63	0.97	0.63
Reeds 4 ²	0.0	-0.15	0.94	-0.15
Reeds 20	0.0	2.02	0.80	1.87
Reeds 20 ²	0.0	-2.57	0.99	-2.12
Trees 1	0.0	0.34	0.64	0.30
Trees 1 ²	0.0	-1.00	1.00	-1.08
Trees 8	0.7	-1.80	0.53	-1.11
Trees 8 ²	0.7	-	0.31	-0.30
Trees 14	1.0	1.97	0.43	1.13
Trees 14 ²	1.0	-	0.43	-1.05
Water Distance	-	-	0.28	-0.03
Water Distance ²	-	-	0.28	-0.11
Settlement Distance	-	-	0.37	0.09

Maputo Females, Wet Season

Variable	Decay	Best model parameter value	Importance	Parameter- averaged value
Distance	-	-0.97	1.00	-0.97
Reeds 2	0.0	0.14	0.81	0.32
Reeds 2 ²	0.0	-	0.58	-0.06
Reeds 18	0.0	-	0.39	0.59
Reeds 18 ²	0.0	-	0.32	-0.24
Trees 0	-	0.36	1.00	0.34
Trees 0 ²	-	-0.25	1.00	-0.24
Trees 14	0.7	-0.72	0.52	-0.65
Trees 14 ²	0.7	-3.20	1.00	-2.94
Water Distance	-	-0.35	0.79	-0.33
Water Distance ²	-	-	0.31	-0.09
Settlement Distance	-	-	0.29	0.04

Maputo Males, Dry Season

Variable	Decay	Best model parameter value	Importance	Parameter- averaged value
Distance	-	-1.07	1.00	-1.07
Reeds 4	0.0	0.81	0.98	0.74
Reeds 4 ²	0.0	-0.34	1.00	-0.33
Trees 1	0.0	0.52	1.00	0.47
Trees 1 ²	0.0	-0.12	0.84	-0.11
Trees 10	0.9	-1.41	0.62	-1.25
Trees 13	0.8	2.35	0.79	1.87
Water Distance	-	0.32	0.91	0.33
Water Distance ²	-	-0.18	0.99	-0.18
Settlement Distance	-	-	0.51	0.11

Maputo Males, Wet Season

Variable	Decay	Best model parameter value	Importance	Parameter- averaged value
Distance	-	-1.04	1.00	-1.04
Reeds 0	-	-	0.33	-0.00
Reeds 0 ²	-	-	0.48	-0.48
Reeds 3	1.0	-	0.35	0.10
Reeds 3 ²	1.0	-0.06	0.46	-0.06
Trees 2	0.0	0.44	1.00	0.43
Trees 9	1.0	-	0.43	0.45
Trees 9 ²	1.0	-0.81	0.99	-0.81
Trees 15	0.7	-	0.32	-0.51
Trees 20	0.6	3.21	0.99	3.13
Trees 20 ²	0.6	1.06	0.53	1.05
Water Distance	-	-0.13	0.66	-0.12
Water Distance ²	-	-	0.32	-0.00
Settlement Distance	-	-	0.28	-0.01

Etosha Females, Dry Season

Variable	Decay	Best model parameter value	Importance	Parameter- averaged value
Distance	-	-1.13	1.00	-1.13
Mopane 1	0.0	0.50	1.00	0.50
Mopane 7	0.0	0.23	0.91	0.24
<i>A. nebrownii</i> 1	0.0	0.21	1.00	0.21
<i>A. nebrownii</i> 18	0.0	-	0.30	0.09
<i>A. nebrownii</i> 18 ²	0.0	0.41	1.00	0.40
<i>Acacia</i> 2	1.0	0.18	1.00	0.18
Water Distance	-	-0.21	0.57	-0.24
Water Distance ²	-	0.18	0.90	0.21

Etosha Females, Wet Season

Variable	Decay	Best model parameter value	Importance	Parameter- averaged value
Distance	-	-1.39	1.00	-1.39
Mopane 1	0.8	0.16	0.85	0.14
Mopane 1 ²	0.8	-0.17	0.97	-0.18
Mopane 15	0.0	-	0.35	0.20
<i>A. nebrownii</i> 0	-	0.35	0.98	0.30
<i>A. nebrownii</i> 0 ²	-	-0.07	0.87	-0.06
<i>A. nebrownii</i> 7	0.0	-0.60	0.85	-0.64
<i>A. nebrownii</i> 7 ²	0.0	0.23	0.84	0.21
<i>A. nebrownii</i> 14	0.0	-0.71	0.81	-0.72
<i>Acacia</i> 2	0.0	0.57	0.99	0.59
<i>Acacia</i> 10	0.0	1.46	0.52	1.31
<i>Acacia</i> 10 ²	0.0	3.11	0.84	2.72
<i>Acacia</i> 20	0.0	-9.20	1.00	-8.02
<i>Acacia</i> 20 ²	0.0	-11.59	0.99	-9.83
Water Distance	-	-0.17	0.48	-0.19
Water Distance ²	-	-	0.30	-0.01

Table 2.1. Candidate scales and decay of each variable chosen for the model selection process for each dataset and their estimated parameter values after model fitting.

Dataset	Multi-scale	Base-scale	Difference
Maputo Females, Dry Season	2901.03	2944.45	-43.42
Maputo Females, Wet Season	2748.15	2779.19	-31.04
Maputo Males, Dry Season	3472.33	3520.81	-48.48
Maputo Males, Wet Season	4112.84	4155.37	-42.53
Etosha Females, Dry Season	11545.80	11561.40	-15.60
Etosha Females, Wet Season	9439.26	9508.14	-68.88

Table 2.2. AIC scores for the best model in each dataset for both the multi-scale and the base-scale versions.

habitat attribute at the candidate scales, e.g. *Acacia* at 20 pixels (Fig. 2.6C). In total, 19 quadratic variables were chosen in the second, model selection step for the multi-scale models, and 8 were chosen for the base-scale models (Table 2.1). By examining the shapes of these quadratic functions over the range of habitat occupied by individuals (icons on Fig. 2.7), we see that in 10 cases the squared term specifies a curvilinear but still essentially monotonic relationship. In 13 cases, a unimodal ‘hump’ is observed (e.g., Maputo females during the dry season for tree density at 1 pixel, or 0.5 km). In 4 cases, we observed a function with an intermediate minimum (e.g., Etosha females during the wet season for *A. nebrownii* at 7 pixels, or 3.5 km). These fitted functional forms guide our interpretation of the behavioral ecology of the elephants (Fig. 2.2).

2.4.3 Variables and scales describing elephant preferences

- **Distance.** The distance parameter was always negative and varied from -0.97 to -1.39. Taking into account the different numbers of available pixels in different distance bands, this corresponds to probabilities of moving 0, 0.5, 1, or > 1 km from the original location of 0.15, 0.37, 0.22, and 0.27 (for parameter -0.97) and

0.28, 0.44, 0.17 and 0.11 (for parameter -1.39). When elephants move locally they prefer to move as little as possible in these reserves.

- **Reeds, Maputo.** When smoothing the reed data, for each elephant group except males in the wet season, a flat kernel ($d = 0$) was optimal for reeds regardless of scale, indicating that all pixels contributed equally. Males in the wet season had a decaying kernel ($d = 1.0$) for reeds at a scale of 3 pixels, indicating pixel influence decreased with distance from the central pixel. The model selection results reveal that at small scales, males avoided reeds in the wet season (3 pixels, or 1.5 km) but had an intermediate preference (maximum at 38% cover) in the dry season (4 pixels, or 2 km). Females had a small-scale preference for reeds in both seasons. However, only females during the dry season had a preference for reeds at the large scale (20 pixels, or 10 km), which was highest at 20% cover. Reeds occur in large stretches that appear homogenous from a distance (i.e. larger scale), but there are small openings within the beds (i.e. smaller scale) where elephants bathe and drink. This may explain why most elephant groups only have a relationship with reeds at a small scale. Reeds indicate the presence of consistently wet areas, so it is not surprising that reedy areas are more attractive for all elephants in the dry season, when water is scarcer elsewhere.
- **Trees, Maputo.** For all elephants in Maputo, a flat kernel provided the best fit for smoothing of tree cover at small scales (up to 2 pixels, or 1 km). At larger scales (> 8 pixels, or 4 km), decaying kernels with d from 0.6 to 1.0 were best (Table 2.1). This pattern suggests a relatively short perceptual range for tree cover. Following model selection, at small scales males in both seasons showed a

positive preference for trees, but for females this was a convex quadratic function with an intermediate optimal tree density of 19% in the dry season and 28% in the wet season. This suggests the base resolution of environmental data used in this study (500 m) might be too large and is already blurring the savannah ‘mosaic’ in Maputo as perceived by females (see Fig. 2.2, Pattern I). Males in both seasons also have a negative relationship with tree density at medium scales (9-10 pixels, or 4.5–5 km), although for the wet season there is a slight intermediate peak. This becomes a positive preference at even larger scales (> 12 pixels, or 6 km). This combination suggests a preference for medium-sized clearings within continuous forest (Fig. 2.2, Pattern C). Females in the dry season show this same alternating preference for tree density at medium and large scales. However, females in the wet season demonstrate a negative relationship for tree density with a slight intermediate peak at a large scale (14 pixels, or 7 km). Overall, these results suggest that elephants like to be near small clumps of trees within relatively open areas, with all groups but females in the wet season willing to venture into more continuous forest.

- **Vegetation, Etosha.** In both seasons, a flat smoothing kernel was optimal for each of the vegetation variables at all scales except in two cases: *Acacia* at a scale of 2 pixels in the dry season and mopane at a scale of 1 pixel in the wet season had decaying kernels ($d = 1.0$ and 0.8 , respectively). Because these habitats are already at a small scale, this indicates that elephants only consider these vegetation types in their immediate vicinity when making habitat choices. Following model fitting, we find that female Etosha elephants preferred higher

densities of mopane and *Acacia* at a small scale in both seasons. They also showed a preference for higher local densities of *A. nebrownii* in the dry season, but intermediate levels in the wet season (43% cover). At larger scales, in the dry season, the elephants favoured mopane at 7 pixels (3.5 km) and *A. nebrownii* at 18 pixels (9 km). In the wet season, they had a u-shaped relationship to *A. nebrownii* at 7 pixels (3.5 km) and a negative one at 14 pixels (7 km), indicating an avoidance of the edges of large patches of *A. nebrownii*. They also had a slight u-shaped relationship with *Acacia* at 10 pixels (5 km) but showed a preference for an intermediate amount of *Acacia* at 20 pixels (10 km). This suggests an avoidance of *Acacia* mosaics but a preference for being near the edge of them. (Note the full-landscape multi-scale map for the Etosha wet season in Fig. 2.8 shows a cluster of observations on the edge of the unfavorable blue area, which is an *Acacia*-dominated mosaic.) Seasonal differences in selection scale are also evident for these elephants: mopane and *Acacia* vegetation contributed much more strongly at a large scale (> 15 pixels) in the wet season than in the dry season (compare Figs 2.6A and C with 2.6D and F).

- **Water.** As a ‘distance to’ variable, the water layer is intrinsically smooth, so there is only one scale. In all Maputo datasets except one, elephants dislike being far from water. Water does not appear at all, however, in the best model for female elephants in the dry season, the dataset in which one might expect it to be the most important. However, Fig. 2.7 shows that all of our data for this period are from the north region of the reserve, which is the region with reeds, a surrogate for water (Harris et al., 2008). In the best model, reeds are positively preferred at

a small scale (4 pixels, or 2 km) and intermediately preferred at a large scale (20 pixels, or 10 km), indicating females like to be on the edge of the reedy areas (Fig. 2.2, Pattern E). Given that, we propose that water does not add much explanatory power compared to when elephants are further south, near the Futi corridor. We note that in the respective base-scale model, which does not allow a large-scale relationship with reeds, water *is* important as expected. In Etosha, elephants stay close to water during the wet season but have a u-shaped relationship during the dry season. For a point resource like a water hole, this suggests individuals are alternately moving to and away from it (Roever, Van Aarde & Legget 2013; Fig. 2.2, Pattern K). This is because in the dry season, vegetation near water holes is rapidly denuded, forcing elephants to travel farther away from water to forage (De Beer et al. 2006). The respective base-scale model demonstrates the same relationship to water.

- **Human settlement, Maputo.** Elephants appear to pay little attention to human settlements in any dataset when fitting multi-scale models, but are important in the base-scale model for females in Maputo during the dry season. In all models in which ‘distance to human settlement’ appears, even models of low rank, its parameter is positive, indicating that, however mildly, these elephants avoided human settlements.

2.4.4 Comparison with base-scale models

For the most part, the vegetation variables that appeared in the best base-scale model for a particular dataset were the same as those that were in the best multi-scale model at a small scale. For example, for males in Maputo during the wet season, the best multi-scale

model included reeds at 3 pixels and trees at 2 pixels; both reeds and trees were included in the best base-scale model. In one case, however, the shape of the relationship changed: females in Maputo during the dry season showed a positive preference for reeds at 4 pixels in the multi-scale model, but had a negative preference for reeds in the base-scale model. Additionally, there were two cases where the two types of models had different variables: reeds in Maputo for females during the wet season and males during the dry season were included in the multi-scale models (at 2 and 4 pixels, respectively) but not in the base-scale models.

2.4.5 Local relative quality predictions

These predictions form the basis of the model fit. Fig. 2.7 demonstrates that the main difference between the multi-scale and base-scale models is that low-quality pixel errors – the left tail of each histogram – are much reduced when smoothed variables are incorporated (white bars) compared to when they are not (black bars). Without smoothing, many parts of these landscapes are locally heterogeneous, with high-quality and low-quality locations closely adjacent. Even when elephants cluster in areas with many high-quality pixels, they are inevitably sometimes found in the interspersed low-quality pixels, perhaps because they are moving between high-quality areas. When smoothing is allowed, these pixels increase in probability of occupation by virtue of their high-quality surroundings.

2.4.6 Landscape-wide relative quality predictions

The landscape-wide relative quality maps generated from the best multi-scale models are, in some cases, strikingly different from those based only on base-scale models (Fig. 2.8). As well as reducing low-quality pixel errors (see above), these maps sometimes reduce

the total area predicted to be high quality that does not contain elephants. Whether elephants are intentionally avoiding these areas, or are present but not being observed, will require further data to test.

For Maputo, the landscape-wide maps that include smoothed variables show the regional distribution of elephants better than maps with only base-scale variables, as indicated by the areas of red pixels. Interestingly, the maps for males show their attraction to the north-south ‘tree corridor’ along the western side of the reserve, whereas the best models for females, when extrapolated into southern regions, suggest they would stay to the east. This difference arises mainly from their different relationships to tree density at various scales.

One exception to the pattern of multi-scale models making better predictions is for Maputo males in the wet season, when individuals sometimes venture into the northeast region of the reserve. This general area is assessed as relatively poor by the multi-scale model, whereas the base-scale model shows it as of medium quality with pockets of high quality. The multi-scale model does well elsewhere, where most observations occur, so presumably fit in those regions was favored.

For Etosha, the multi-scale and base-scale maps are similar in the dry season, and both classify regions where female elephants occur as high quality. The multi-scale map reduces the more minor of the two errors: there are fewer high-quality regions without elephants. For the wet season, the maps are very different. The base-scale map has mixed performance, with individuals found in regions classified from low quality (north-central and southern tip) through high quality. There are also extensive ‘high quality’ regions with no records of elephant presence. Overall, the base-scale map does not reflect the

observed presence of elephants well. But once we allow smoothing the situation changes, and the multi-scale model indicates that a) elephants seem to avoid the two *Acacia*-dominated regions (even though they like *Acacia* on a local basis), and b) within the rest of the reserve, many large areas are suitable, allowing females to roam widely in a way that isn't observed during the dry season.

2.5 Discussion

We use the data-driven smoothing approach presented here to identify the spatial scales at which an organism selects habitats. By smoothing each variable independently, we were able to identify its optimal scale(s) and improve model fit (Fisher, Anholt & Volpe 2011). We add support to the proposition that organisms select habitat variables within the landscape at varying scales (Bowyer & Kie 2006; Mayor et al. 2009). Selection depends on the spatial context of the variables (Duchesne, Fortin & Courbin 2010).

Including squared values for variables in the model selection process allows for situations where an organism prefers an intermediate value of a particular variable (such as tree cover), or where it is moving towards and away from point features and/or avoiding edges of vegetation. These relationships occurred in our models, emphasizing the importance of using flexible resource selection functions in habitat analyses.

The predictions made by our base-scale models are in general agreement with those of Harris et al. (2008): elephants prefer to be close to water, within forage, and away from people. In the previous paper, the distance variables were the only smooth variables, possibly giving them greater predictive power compared to the other base-scale variables. In our multi-scale models, the signal of water preference is lost in some datasets, likely due to the inclusion of other, smoothed variables (like proportion of

reeds) that signify water availability and possibly other landscape qualities. In two instances, distance to water is *added* to the best multi-scale model: males in Maputo and females in Etosha during the wet season. This is not evident in the landscape-wide quality maps, but there is still local variation in the quality of the habitat that is partly dependent on the distance to water.

Some habitat variables operate on multiple scales in opposing fashion, such as *Acacia* for females in Etosha during the wet season being selected positively at a small scale (2 pixels, or 1 km) but preferred in intermediate amounts at larger scales (20 pixels, or 10 km; Fig. 2.7). This indicates that individuals avoid regions dominated by *Acacia* (only selecting the edges) but favor isolated *Acacia* patches within other regions (Fig. 2.2, pattern E). But even at the smallest scale (for our study, a 500 m x 500 m area), the selection of a variable may be due to its association with a resource preferred at finer scales not captured by our data (e.g., presence of water). Additionally, in Maputo, males in both seasons and females in the dry season have a similar relationship to trees: positive preference at a small scale (intermediate preference for females), negative preference at a medium scale and positive preference again at a large scale (Fig. 2.7). Since the tree variable in Maputo is the proportion of closed woodland, and not divided into types, elephants might select certain tree types against others. For instance, elephants may prefer one type of tree at a small scale but select for clearings within another type, resulting in the opposing preference patterns at medium and large scales (see Fig. 2.2).

We also discovered that over-smoothing is a potential problem in performing these analyses. We initially extended the smoothing radius to > 100 pixels (50 km), and found that there were often peaks (or even steadily improving) AIC values in this region.

When smoothing occurs at this scale, environmental data tend to change monotonically across the entire landscape. In that case, there is a risk that any slight bias in the mean movement (i.e., any drift in the overall locations of animals), *whatever the cause*, will likely show up as a preference for, or avoidance of, that variable. This reflects the general truth that the spatial autocorrelation inherent in smoothed data will increase the degree of apparent correlations between variables, meaning that one must be very careful about assigning cause and effect. As our suburb/city example illustrates, when considering large-scale preferences, variables may act as proxies for something else. Because of these potential problems, we suggest using a maximum smoothing radius no more than twice the size of the choice radius of local movements. Smoothing only up to the choice radius precludes individuals from perceiving the environment at distances greater than they can travel.

We expected to see differing responses between male and female elephants, since females are typically part of a mixed herd containing juveniles that are less mobile than adults, while males are often solitary and can move larger distances (Smit, Grant & Whyte 2007). However, while our data on males covers a greater spatial extent, differences in preference are quite small – even when males occupy regions for which we have no female data, their preferences remain similar. This suggests that our findings are reasonably robust, even though the elephant movements in this analysis do not encompass the entirety of each reserve's landscape.

This study demonstrates that incorporating multiple spatial scales improves predictions of species habitat preferences, and as a consequence may dramatically alter landscape-wide maps of habitat quality. Discovering these habitat preferences helps

identify the resources required by the species, at the correct scale, allowing wildlife managers to provide or restore them. The habitat preference maps help conservation planners ensure that enough habitats remain available, and accessible, for the target populations. For elephants, this is especially critical, given proposals that would allow protected populations greater freedom to roam (Van Aarde, Jackson & Ferreira 2006; Van Aarde & Jackson, 2007).

Chapter 3

Understanding habitat preferences of brown bears in a complex landscape by using lasso to inform model selection

3.1 Summary

Understanding the selection and use of habitat by animals is important for their conservation and management. This becomes challenging when individuals are faced with different habitat choices due to the presence of neighboring individuals and/or the finely heterogeneous nature of their surrounding environment. Additionally, individuals may perceive their environment at different spatial scales than that of the data source, e.g. satellite imagery. In this study, we expand upon a previously developed method of incorporating multiple spatial scales into habitat selection models to identify habitat preferences and generate habitat quality maps for brown bears (*Ursus arctos*) on the Kenai Peninsula, Alaska. Because of the complexity of the landscape, the process of generating multiple spatial scales resulted in too many predictor variables to be able to fit all model combinations. Instead, we used the least absolute shrinkage and selection operator (lasso) to rank each predictor variable in order of importance. We then fit models of increasing complexity and compared them using AICc. We included a parameter that describes the distance between the available habitat and the nearest neighboring bear to assess the influence of neighbors on habitat selection. We successfully identified the appropriate spatial scales and habitat variables used by brown bears within different parts of the landscape. The inclusion of the neighbor distance

parameter did not alter the relative importance of any predictor variable but did improve model fit for some groups of bears, namely those inhabiting the higher-elevation mountain ranges. The resulting habitat preference maps identified regions of high-quality habitat and can be used to reduce bear-human conflict on the Peninsula. This method is widely applicable to any study in which there are a large number of predictor variables, and it is particularly useful given the recent emphasis on the inclusion of multiple spatial scales in habitat selection studies.

3.2 Introduction

Understanding the complex process of how and why animals move throughout a landscape is a challenge. In some cases it is also a matter of pressing importance. The population of brown bears (*Ursos arctos*) on the Kenai Peninsula of Alaska has been given ‘special concern’ status due to declining numbers and increased human development (Suring & Del Frate 2002; Goldstein et al. 2010). By using their movements to discover which aspects of their landscape bears value most, we can minimize human-bear conflicts.

Individuals utilize specific habitats within their landscape to obtain resources. Resource selection functions (RSFs) are often used to determine which habitats individuals prefer over others (Manly et al. 2002). RSFs provide the relative probability of use of different habitat types by an animal and can be evaluated using conditional logistic regression (Manly et al. 2002; Duchesne, Fortin & Courbin 2010). In addition to the presence of resources, interactions such as competitive exclusion can also affect the quality of a particular habitat patch. In this population on the Kenai Peninsula, individual bears may be constrained in their movement by neighboring bears. Consider the simplest

case, where a single bear is present on the Peninsula and has access to every part of the landscape. The preferences of this individual bear could be obtained straightforwardly with an RSF. However, consider the other extreme, where the entire Peninsula is saturated with brown bears, and each bear stays within a box-shaped home range that is bordered on all sides by the home ranges of other bears. In this case, each bear is limited in its choice of available habitat, so preferences for each bear can only be determined within its home range (Thomas & Taylor 2006). In addition, this distribution may prevent some individuals from selecting optimal habitat that occurs within the home range of a neighboring bear (Fretwell 1972). Therefore, it is difficult to determine the general preferences of all individuals in the population because each is faced with different habitat choices. The actual population of brown bears on the Kenai Peninsula lies somewhere between these two extremes. Most individual bears stay within a small area of the landscape for much of the year, and their home ranges do not greatly overlap with those of other bears. Therefore, each individual's habitat choices are potentially restricted by the presence of their neighbors.

Complex landscapes, which can be very finely heterogeneous and have a multitude of different habitat types, can also limit individuals in their habitat choices and make it difficult to determine habitat preferences. Each prominent environmental feature that is potentially important to bear movement, such as coniferous forest cover or elevation, must be mapped; the resulting landscape-wide maps are used as predictor variables when assessing habitat selection. When the number of predictor variables is small, all possible combinations can be evaluated (as in Whittingham et al. 2006). The best model(s) containing the most important variables can then be identified using

information-theoretic approaches such as Akaike's Information Criterion (AIC; Anderson & Burnham 2002; Burnham & Anderson 2002). Recent techniques have begun to incorporate environmental information on a continuum of spatial scales to identify those that an organism is choosing (De Knecht et al. 2011; Fisher et al. 2011; Mashintonio et al. 2014). When this is applied to complex landscapes, which already have a multitude of predictor variables, the number of model parameters becomes even greater, making it computationally difficult to compare all models. Often, when the number of predictors is high, only a subset of all possible models is selected for evaluation (McLoughlin, Coulson, & Clutton-Brock 2008). Candidate models may be chosen following a preliminary analysis to identify correlation among variables (Compton, Rhymer, & McCollough 2002; Roeber, Van Aarde & Leggett 2012) or by using ecological knowledge (Gustine et al. 2006). However, the additional spatial scales of a single environmental feature are derived from the original landscape map, making it difficult to decide *a priori* which combinations of predictor variables should be included for model selection.

The selection of the correct predictor variables has not traditionally been considered a problem in habitat selection studies, but it is a common issue in other fields, i.e. when assessing risk factors of pharmacological drug use (Avalos et al. 2011), or for selecting important genes out of large genome datasets (Li et al. 2011). One approach for determining the important predictor variables out of a large set is the least absolute shrinkage and selection operator (lasso). Similar to model selection via AIC, this method also provides a model with the optimal number of predictor variables (Reid & Tibshirani 2014). For our application, however, this proved problematic; optimal models varied

from one to dozens of predictors, which limited their application to the understanding of bear preferences. We therefore used a hybrid approach in which the rankings of predictor variables provided by the lasso method determined the sequence of variables entered into a model selection process based on AIC corrected for small sample size and a large number of predictors (AICc; Hurvich & Tsai 1989). We implemented this technique to understand the habitat preferences of brown bears from the Kenai Peninsula, Alaska. This study expands our methodology for incorporating spatial scale that was first introduced in Mashintonio et al. (2014). Unless stated otherwise, all analyses were performed using *Mathematica* software (Wolfram Research 2012).

3.3 Methods

3.3.1 Study site

The Kenai Peninsula (c 23,000 km²), located in south-central Alaska (Fig. 3.1a), is bordered by Prince William Sound to the east, the Gulf of Alaska to the south, and Cook Inlet to the west (Goldstein et al. 2010). The eastern two-thirds of the peninsula is dominated by the Kenai Mountain Range, which rises to 1,990 m (Goldstein et al. 2010; Fig. 3.1b). The western portion of the peninsula is the Kenai lowlands landform, a glaciated plain with numerous lakes and streams (Goldstein et al. 2010; Fig. 3.1b). During the time of this study there were between 250 and 300 brown bears on the Peninsula (Suring & Del Frate 2002).

3.3.2 Location data

Bear location data were provided by GPS collars, which took fixes every six hours. Thirty-three females were collared between 1997 and 2004. Each movement was

represented by a pair of starting and ending x, y coordinates. We only considered movements that ended greater than 10 pixels (5 km) away from frequently visited streams because of the potentially confounding effects of bears' oscillatory movements towards and away from streams. During these movements, bears may visit streams without regard to the habitat through which they are passing, making it more difficult to discern their preferences elsewhere. We further restricted movements to those that ended less than 5 km from the starting location because we wanted to analyze only shorter movements in the "encamped" mode (which we infer as local foraging) as opposed to faster, long-distance movements in the "exploratory" mode (movement to distant fishing spots, etc.) (Morales et al. 2004; Roever et al. 2013; Mashintonio et al. 2014).

Differing resource availability throughout the year can lead to seasonal variation in habitat selection (Dahle et al. 1998; Persson et al. 2001; Nielsen et al. 2002; Nielsen et al. 2003; Martin et al. 2013). Therefore, we partitioned each year of bear data into three seasons and computed separate RSFs for each (McLoughlin et al. 2010): spring (den emergence – 15 June), summer (16 June – 15 August), and fall (16 Aug – den return). After den emergence in the spring, bears typically consume large amounts of new herbaceous vegetation and old berries (Dahle et al. 1998; Persson et al. 2001; Suring et al. 2006). Salmon begin to return to streams to spawn in mid-June and are an important food source for brown bears (Hilderbrand et al. 1999; Jacoby et al. 1999; Belant et al. 2006; Suring et al. 2006). Prior to returning to their winter denning sites, bears eat large amounts of berries and roots to prepare for hibernation (Dahle et al. 1998; Munro et al. 2006; Suring et al. 2006; Nielsen et al. 2010).

3.3.3 Environmental data

We used raster layers of vegetation and elevation as predictors of bear movement. The vegetation layers included the proportions of alpine vegetation (alpine), wetland vegetation (wetlands), coniferous forest (conifer), deciduous forest (deciduous), mixed forest, alder and willow trees (alder/willow), and spruce trees (spruce). All layers had a pixel size of 500 m by 500 m. These layers had the highest proportions throughout the Peninsula and were thus chosen out of a much larger set. We standardized each variable to have zero mean and unit standard deviation. We did not use principal component analysis (PCA) to further reduce the number of variables for reasons discussed below.

3.3.4 Cluster analysis

Due to the complex, finely heterogeneous nature of the landscape and the localized movement of individual bears, each bear's choice of habitat may be markedly different depending on the area that it inhabits. This can limit our ability to make generalized predictions across the entire landscape. To account for this, we performed a cluster analysis to partition the Peninsula into regions of relatively similar vegetation makeup (Steinley 2006). We only included areas within 50 pixels of a known bear location to prevent the inclusion of habitat that may have been different from the habitats visited by bears in this study. We wanted to achieve relatively contiguous spatial regions so that the movements of a given bear would generally fall within one region, so we first smoothed the vegetation variables using a 10-pixel radius kernel to remove local heterogeneity and reveal regional patterns. We then constrained a K-means clustering algorithm to produce no more than five clusters. This produced four relatively homogenous clusters with clear spatial contiguity, two in the lowlands and two in the highlands, and a fifth cluster

holding rare and marginal vegetation mixtures (Fig. 3.1c). Each individual bear movement was grouped according to the region in which it was located, and any movements that ended within the fifth cluster were discarded.

3.3.5 Conditional logistic model

Each individual movement i is influenced by the values of all possible destination pixels j , each of which has a vector of k potential predictor values \mathbf{x}_j derived from the environmental raster layers. A distance term between the current location and each potential destination pixel was included in these values to represent the cost of movement (Hjermann 2000; Harris et al. 2008). The choice \mathbf{y}_j was represented as a binary response in which the chosen destination was assigned a value of 1, and all other locations within a small radius of the start location were assigned a value of 0. The complete dataset for a single movement was stored as a matrix \mathbf{X}_i and a binary column vector \mathbf{y}_j that included the destination pixel and all pixels within a 10-pixel (5 km) radius of the starting pixel.

Under the conditional logistic model, the probability p_j that an animal chooses a pixel j as the next location is

$$p_j = \frac{e^{x_j\beta}}{\sum_j e^{x_j\beta}}$$

where β is a k by 1 vector of parameters to be estimated. The log-likelihood of an individual movement L_i is simply the logarithm of the value of p_j for the chosen destination pixel (where $y_j = 1$), and the log-likelihood of the entire dataset is the sum of the L_i over all movements i . We used conditional logistic regression to fit all models of habitat selection. We illustrated model fit by using the pixel values given by p_j to generate relative local quality preference maps for each dataset (see Fig. 3.2 for example;

Mashintonio et al. 2014). The parameter estimates were applied to the local neighborhoods around each starting location. Fit was visually assessed by overlaying each map with movement end-points to determine how well our models predicted movement choices.

3.3.6 Choosing optimal smoothing scales

RSFs have been increasingly used to incorporate spatial scale into the study of an individual's habitat preferences (Boyce 2006; De Knecht et al. 2011; Fisher et al. 2011; Mashintonio et al. 2014). However, researchers often only select a few scales at which to analyze animal movement. This can limit model inference and lead to mismanagement of targeted species if the chosen scales are not biologically relevant for the species in question (Levin 1992; Boyce 2006; Mayor et al. 2009; Wheatley & Johnson 2009; De Knecht et al. 2010; De Knecht et al. 2011). Instead, habitat selection should be assessed on a continuum of scales to identify the ones that an organism is choosing (Fisher et al. 2011; Mashintonio et al. 2014).

To generate multiple spatial scales, we smoothed each vegetation variable individually by averaging each pixel with its neighboring pixels within an increasing radius, up to 20 pixels (10 km; Mashintonio et al. 2014). We included squared versions of each variable at each radius, or scale, to allow for non-linear preference functions, particularly those in which an intermediate level of a variable is preferred (Johnson et al. 2004; Johnson & Gillingham 2005; Mashintonio et al. 2014). Pixels representing non-habitat (i.e., ocean) were not included in the average (Mashintonio et al. 2014).

At each radius for each variable we fit four models: one with the distance from current location as the only parameter, one with distance and the variable, one with

distance and a squared version of the variable, and one with distance and both the linear and squared versions of the variable (Mashintonio et al. 2014). We compared models of differing complexity using AIC. We generated four lines of AIC values, one for each model, over every smoothing radius. Candidate scales were chosen by looking for local minima in the AIC scores, but in the figures we inverted the y-axis so that we instead were looking for peaks (Fig. 3.3a; Mashintonio et al. 2014).

Each variable at the selected scale was then further optimized by the addition of the linear decay parameter d , which determines how heavily each pixel should be weighted in the average depending on its distance from the central pixel (Mashintonio et al. 2014). This takes into account differences in the way an individual integrates its surroundings, such as declining perceptual abilities due to obstructing vegetation (Harris et al. 2008; Mashintonio et al. 2014). For a flat smoothing kernel, all pixels are weighted equally within the given radius ($d = 0$). We ranged d from 0 to 1 in steps of 0.1 (Mashintonio et al. 2014).

The smoothing process resulted in a large number of predictor variables for each dataset. PCA can be used to reduce the number of variables by transforming them into new variables, which are ordered so that the first variable captures most of the variation present in the data (Jolliffe 2002). One drawback of PCA is that the new variables can be harder to interpret; in our case, this technique also interfered with the smoothing process. It was often the case that layers of the same variable at different scales were reduced together into a principal component, thus counteracting the effect of smoothing. We therefore maintained all of the selected scales throughout the model fitting process.

3.3.7 Interpreting combinations of scales

Individuals may have a positive or negative preference for a particular habitat variable at any scale; the inclusion of squared terms also allows for non-linear preferences. However, when individuals have different relationships to the same habitat variable at different scales, it can be unclear what their true preferences are. Mashintonio et al. (2014) interpreted different combinations of preference function shapes as they pertained to elephants; the same interpretations can apply here. Individuals with a negative preference for a habitat variable at one scale but a positive preference at a larger scale are inferred to prefer clearings within that habitat roughly equal to the size of the radius of the smaller scale smoothing kernel. Individuals with a positive preference for a habitat variable at one scale but a negative preference at a larger scale prefer isolated clumps of the habitat roughly equal to the size of the radius of the smaller scale smoothing kernel. When there is a hump-shaped preference function for a habitat variable at a small scale, it is possible that the scale of the raw data is already too coarse to determine an accurate preference, or that individuals may like a mosaic of the habitat or the edge of the habitat rather than continuous cover. A u-shaped function at larger scales suggests an avoidance of the edge of the habitat, or a preference to be either within or outside of that patch of habitat. For point or linear features coded as a ‘distance from’ layer, a hump-shaped function indicates that individuals keep a fixed distance from the feature, and a u-shaped function means they alternate moving towards and away from the feature.

3.3.8 Neighbor distance

It was observed from the movement data that most individual bears on the Kenai Peninsula only occupy a small part of the landscape and do not travel much beyond this

area for most of the year. Furthermore, the ranges of many individuals appear to be bordered by ranges of nearby conspecifics (Fig. 3.1d). When organisms select habitat, it is assumed that the habitat selected is of high quality and increases individual fitness (DeCesare et al. 2014). However, neighboring bears may potentially constrain an individual from selecting high-quality habitat that occurs outside of its range and force it into sub-optimal habitat (Fretwell 1972).

To incorporate this effect we created a ‘distance to nearest neighbor’ layer by computing the distances from each potential destination pixel within a local neighborhood of movement choices to the nearest GPS location of another individual. We only considered fixes taken +/- 24 hours of the fix of the focal individual as potential neighbors; movements where there were no neighboring individuals within that interval were not included in the analysis. This layer was used as a predictor variable along with distance from current location, elevation, and the optimally chosen scales of vegetation layers to determine if it changed the model parameters and improved model performance compared to models that did not include this layer.

3.3.9 Lasso and model selection

We used conditional logistic regression with lasso penalties to fit models of habitat preference. Model complexity is controlled by the regularization parameter λ ; as $\lambda \rightarrow \infty$, no variables are in the model (all parameter estimates are 0), and when $\lambda = 0$, all variables are in the model (Avalos et al. 2011). As λ increases from 0, the parameter estimates begin to shrink; those of the less important variables will shrink to 0 before those of the more important variables. This process produces a relative ranking of importance for the entire set of predictor variables.

The first model fit for each dataset was at the smallest λ value where all parameter estimates were zero (Reid & Tibshirani 2014). Models were then fit at 300 additional λ values that decreased logarithmically to the minimum λ , which was found by multiplying the first λ by 0.000001 (Fig. 3.3b). All lasso fits were performed in R using the package ‘clogitL1’ (Reid & Tibshirani 2014).

We initially performed K-folds cross validation to determine the optimal λ value and thus the important variables and their parameter estimates (Reid & Tibshirani 2014). Under this approach, all movement strata were partitioned into $K = 10$ folds, and one fold was randomly selected to be left out over every value of λ . The conditional logistic regression model was then fit to the remaining strata, and its deviance was compared to the deviance of a model fit using the left-out strata (Reid & Tibshirani 2014). The graph of the difference in deviance between the two models at each λ value is drawn with two vertical lines: the leftmost at the λ with the minimum deviance, and the other at the λ value one standard deviation away from the minimum (Fig. 3.3b). Within this standard deviation, the model with fewer parameters (larger λ value) is considered better. However, this occasionally resulted in a model in which only one parameter, distance from current location, was included, and all other parameter estimates were zero. This type of result was unable to provide insight into the preferred habitat of brown bears.

Alternatively, we used the results of the lasso fit to determine which combinations of variables to enter into a model selection process. We began by fitting a model that only included the most important variable, which was always distance from current location. We subsequently added a single variable to each model in order of importance as determined by lasso; this resulted in a number of models equal to the number of predictor

variables for each dataset. Models were compared using AICc. We expected a plot of AICc scores to follow a u-shaped pattern, where initially the addition of important predictor variables increases model performance, and then the addition of nuisance variables decreases model performance. The model with the minimum AICc score most accurately described bear preferences.

To assess the effect of neighboring individuals on habitat selection, we repeated our analysis and included the neighbor distance layer. This layer was added prior to the lasso stage to allow it to change the ranking of the other predictor variables, and hence the model sequence evaluated using AICc. We had two expectations: 1) models with neighbor distance would have lower AICc scores than models with the same number of model parameters but without neighbor distance, and 2) the best model overall as selected by AICc would include neighbor distance. Fig. 3.3 shows the entire process of scale selection, lasso, and cross validation for a reduced dataset.

3.3.10 Preference maps

We created habitat preference maps for each landscape cluster in each season using the parameter estimates for the environmental variables from the model with the lowest AICc score. Pixel values were given by $e^{x_j\beta}$ to illustrate relative landscape-wide quality (Mashintonio et al. 2014). We began by interpolating these preferences to pixels in the cluster that had variable values within the distribution of the values chosen by bears; this was to prevent extrapolation to pixels with extremely small or large amounts of a particular variable that bears did not encounter within their local neighborhood of movement choices. When included, these extreme pixels can skew the distribution of the quality of the remaining pixels. This process often removed a large percentage of the

pixels within the cluster, so we extrapolated preferences to pixels with values closest to the largest and smallest chosen values until at least 65% of the pixels were included. Movement end-points were overlaid onto the map to assess their ability to predict the landscape-wide distributions of bears.

The landscape-wide maps include a 10-pixel buffer around frequently visited streams. We did not use movements within this buffer, so our models do not apply to them. Habitat within these buffers may be considered low quality by our model and yet still have a high density of bears that are only there to visit the stream. To test this, we compared the extrapolated quality of movement end-points within these buffers to those from the surrounding landscape.

3.4 Results

3.4.1 Landscape cluster analysis

Of the five cluster regions, two were located primarily in the Kenai Mountain Range and two in the western lowlands. The fifth consisted of various less common vegetation combinations, most of which were located on the periphery of the other regions. The “Highland Valleys” region is located within the valleys of the mountain range and is composed primarily of conifer and alder/willow with some alpine, mixed forest and spruce. The “Highland Peaks” region is dominated by alpine, alder/willow, and some conifer and includes one higher elevation mountaintop within the lowlands. The “Lowland Coast” region contains deciduous, mixed forest, spruce, and wetlands. The “Lowland Plains” region has less deciduous, with mixed forest, spruce, and wetlands being joined by alder/willow.

3.4.2 Bear preferences

- Distance.** The distance parameter was negative in all datasets and ranged from -0.94 to -1.43 in the best models. This corresponds to probabilities of 0.29 and 0.10, respectively, of moving >1 km per 6-hour interval. Bears therefore select habitat that is close to their current location.
- Elevation.** Bears in the Highland Valleys are found across a wide range of elevations, but most often between 400–600 m in the spring and 0–200 m in the summer and fall. In all seasons, bears consistently select areas that are lower in elevation than their current location (i.e., while foraging, they are more likely to go down than up). Bears in the Highland Peaks also cover a range of elevations, and in the spring may be found as low as 300 m, but in the summer and fall they generally stay between 700–800 m and 500–600 m, respectively. These bears also select areas that are lower in elevation than their current location in the spring and summer but select intermediate levels of elevation in the fall. Bears from the highlands thus separate the most during the summer. Lowland Coast bears are found between elevations of 0–500 m in the spring and prefer to move upwards. In the summer they are found between elevations of 0–120 m. During the fall, these bears select intermediate levels of elevation, with a peak around 80–100 m. Lowland Plains bears only have a relationship with elevation in the summer, where they are found ranging from 20–180 m and are moving downwards (Fig. 3.4).
- Habitat, Highland Valleys.** During the spring, bears inhabiting Highland Valleys prefer alder/willow locally, clumps of alpine, clearings within conifer, and local

mosaics of deciduous, mixed forest, and wetlands. During the summer, these bears select spruce locally, clumps of alpine, local mosaics of deciduous and mixed forest, and large-scale regions of alder/willow while avoiding wetlands and conifer. During the fall, they like alder/willow at multiple scales and the edge of alpine but generally avoid conifer, mixed forest, spruce and wetlands locally (Fig. 3.4).

- **Habitat, Highland Peaks.** Bears inhabiting Highland Peaks avoid wetlands at various scales in all seasons. During the spring, these bears select alder/willow and conifer at small scales, clumps of mixed forest, and the edges of alpine but avoid spruce and deciduous. In the summer, individuals prefer clearings within alder/willow, mixed forest at multiple scales, and clumps of alpine, conifer, deciduous, and spruce. During the fall, these bears prefer alder/willow at a small scale, deciduous at multiple scales, clumps of alpine, conifer and mixed forest, and clearings within spruce (Fig. 3.4).
- **Habitat, Lowland Coast.** During the spring, bears in the Lowland Coast select conifer and spruce locally, clearings within deciduous, and clumps of mixed forest, and they avoid wetlands locally and large-scale alder/willow. During the summer, these bears like alder/willow, alpine, and wetlands at various scales, clumps of deciduous and mixed forest, and mosaics of conifer and spruce; they also avoid large regions of spruce. In the fall, individuals prefer alder/willow and alpine locally, clumps of conifer, and clearings within deciduous, mixed forest, spruce, and wetlands (Fig. 3.4).

- **Habitat, Lowland Plains.** In the spring, individual bears in the Lowland Plains select alder/willow, mixed forest, spruce and conifer at various scales but avoid wetlands locally. In the summer, bears prefer mixed forest and spruce at small scales. In the fall, they like spruce, a local mosaic of alder/willow, and clearings within deciduous and wetlands (Fig. 3.4).
- **Neighbor distance.** The neighbor distance parameter was negative for all datasets and ranged from -0.01 to -0.12 when it was present in the best model. When this parameter improved model fit, the $\Delta AICc$ score between the best model and the best model without neighbor distance was between 1.5 and 20.4 (Fig. 3.4). For bears inhabiting Highland Valleys, the inclusion of neighbor distance improved model performance during the summer and fall, but not in the spring. The inclusion of neighbor distance also improved model performance for bears in the Highland Peaks in all seasons and the Lowland Coast in the fall. Neighbor distance did not improve model performance for bears from the Lowland Plains in any season. Despite improving model fit, no predictor variables were added or removed to the best model when neighbor distance was present.

3.4.3 Habitat quality predictions

In all maps, pixels were scaled from red (high quality) to blue (low quality). Darkly shaded pixels had landscape values that were too extreme to be included in the extrapolation. The landscape-wide relative quality maps predict broad areas within each region that are expected to represent the quality of the habitat based on the preferences of brown bears in each season (Fig. 3.5). In the spring, the best of the highland regions are composed of alpine vegetation, particularly when it also includes alder and willow, and

the conifer and spruce dominated valleys. Areas with a high proportion of spruce and mixed forest were the highest quality habitat in the lowland regions. During the summer, the majority of the valleys have reduced pixel quality compared to the spring, but the higher elevation alpine habitat is of similar quality. High-quality habitat is less widespread in the lowlands during this season but is still composed of spruce and mixed forest as well as some patches of wetlands along the coast. The highland regions in the fall have similar areas of high-quality habitat in the summer. The lowlands contain more widespread high-quality habitat than during the summer, including areas with a high proportion of mixed forest but not areas with wetlands or deciduous forest.

In all seasons, the quality of the most frequently chosen locations within the 10-pixel radius of frequently visited streams (Fig. 3.6, black bars) was lower than those chosen away from streams (Fig. 3.6, white bars). Bears away from streams more frequently chose locations with a pixel quality greater than 0.7 in all seasons. Bears near streams most frequently chose locations with a pixel quality between 0.3 and 0.6 in the summer and fall; during the spring, they chose higher quality pixels with increasing frequency, peaking between 0.7 and 0.8.

3.5 Discussion

This study successfully incorporates multiple spatial scales for a large number of predictor variables into models of habitat selection by brown bears. Fitting all possible models and comparing them via AICc to determine the important habitat types and scales would be computationally unmanageable. However, we used the rankings of the predictor variables generated by the lasso method to determine which variables to enter into model selection via AICc. This reduced the number of models to fit while still maintaining the

variables that were expected to be important for bears. We recommend this hybrid approach when the number of parameters is too high to fit all possible models.

Local alpine vegetation is important for all highland bears in every season except during the spring for bears in the Highland Peaks, when vegetation at this altitude may not have yet emerged and individuals instead prefer to be on the edges of alpine regions. Lowland Plains bears did not select alpine habitat during any season, but Lowland Coast bears did prefer alpine vegetation during the summer and fall. The importance of this variable increased and the scale decreased from summer to fall, which may indicate the bears' transition towards winter denning sites in higher altitudes.

Despite its widespread distribution throughout the Highland Valleys, bears in this region avoid coniferous forest in all seasons at varying small to medium scales. These bears instead prefer mosaics of both mixed and deciduous forests at similar scales. Even though conifers are less widespread, bears in the Highland Peaks prefer coniferous forests locally in all seasons as well as local clumps of mixed and deciduous forests. The importance of local deciduous forests for these bears is surprising, given that this habitat is almost nonexistent throughout the Highland Peaks. Similarly, local coniferous forest is also very important for bears in the lowlands during the spring despite its rarity within this region. These rare habitats may be an important source of old berries prior to the emergence of new herbaceous vegetation in the spring, while deciduous forests continue to be important throughout the year for their vegetative understories.

Highland bears only seem to prefer spruce habitat during the summer; bears found in the valleys and on the peaks either have no preference or actively avoid spruce during the other seasons. Summer is when salmon are most abundant within streams, so bears

that are not found near streams during this season may utilize the resources found within stands of spruce as an alternative. In contrast, all lowland bears prefer spruce habitat at varying scales during all seasons except for the fall, when Lowland Coast bears select clearings within spruce forest. The majority of the spruce habitat is found throughout the lowlands, so it is unsurprising that it is more important for bears within this region.

Wetlands occur throughout the lowlands of the Kenai Peninsula, but they are only preferred locally during the summer by bears in the Lowland Coast. This habitat is actively avoided in the spring, and lowland bears select clearings within wetland regions in the fall. Sedges are an important component of bears' summer diet and are most abundant in association with tidal wetlands [check McCarthy 1989]. Bears that are not found near streams may instead visit wetlands to obtain resources like sedges, along with small mammals such as voles. There are some wetlands found in the highlands as well, primarily within the valleys. Here, it is preferred during the spring but avoided in the summer and fall. Wetlands may provide a source of new spring growth that is not found elsewhere, leading to its selection during the early portion of the year.

Cross-validation of conditional logistic regression fit using lasso penalties to determine the optimal λ appears to be too conservative in some cases, particularly when it calculates a large standard deviation that reduces the best model to a single variable. In two of 12 datasets, the λ with the lowest deviance plus one standard deviation corresponded to a model with one variable: distance from current location. This was the most important parameter in all datasets and is generally a strong and consistent predictor of animal movements. We used AICc to find a final model that was less restrictive of parameter inclusion. AICc revealed that several landscape variables with parameter

estimates that were reduced to zero in the best lasso model were actually highly important in understanding bear habitat.

In each dataset, most of the candidate predictors were variables smoothed at spatial scales larger than that of the original environmental layers. In the final models, at least one variable in all but two datasets were selected or avoided at more than one spatial scale. These results support the proposition that organisms select habitat at multiple spatial scales (Bowyer & Kie 2006; Mayor et al. 2009; Mashintonio et al. 2014).

The inclusion of the neighbor distance parameter improved model fit for all but one of the highland bear datasets but only one of the lowland bear datasets. Additionally, bears in the Highland Valleys had the largest $\Delta AICc$ score of any datasets, indicating that the inclusion of this parameter had the greatest positive effect. Highland bears are more constrained in their movements because of the steeper elevational gradient and because of their overlapping ranges with other bears. Highland Valley bears in particular had less contiguous habitat than bears in the other regions, requiring these individuals to actively avoid each other more so than in any other group. Lowland bears had more continuous habitat through which to travel and were not found as close to each other, so they did not need to select habitat that was locally farther from their neighbors.

Despite improving model fit in these datasets, including neighboring bears did little to impact the other parameters of the best models. When another variable's ranking or importance did change, it was not enough to be included in the best model. The lack of change among the important variables implies that it is possible to determine the correct habitat preferences of individuals in this habitat, even if they have unknown neighbors.

The presence of conspecifics should still be incorporated into models of habitat selection if there is the possibility that they can affect an individual's habitat choices.

Bear movements within 5 km of frequently visited streams were not included in the fitting process; we did not expect these movements to carry a strong signal of habitat selection due to their nature of being stream-directed. Extrapolation of our models to the locations chosen near-stream revealed that they were generally of lower quality than locations chosen away from streams, which was expected (Fig. 3.6). However, bears found near streams during the spring chose higher-quality locations with more frequency than during either the summer or the fall. Salmon have not yet returned to the streams to spawn during the spring, so individuals may be somewhat selective of their habitat at this time. Alternatively, bears are more commonly found in mid-quality habitat during the summer and fall, when salmon are an important component of their diets (Ben-David, Titus & Beier 2004; Belant et al. 2010). Therefore, the quality of the chosen habitat does not seem to be as important to these individuals as simply being near a stream.

Habitat preference maps can be useful tools for conservationists and managers of threatened species. These maps must accurately reflect the preferences of individuals to correctly predict areas of high use. The incorporation of spatial scale has been shown to improve habitat preference maps for elephants (Mashintonio et al. 2014). By applying the same methodology to identify the relevant scales of bear preferences, we created bear preference maps across the Kenai Peninsula in each season that indicate high-quality habitat, which may reflect the most likely areas that bears can be found. However, these maps were created using the data available to us and may not be indicative of every bear on the Peninsula. Furthermore, the quality of the habitat was scaled from 0 to 1, so the

maps should be interpreted as the *relative probability* of encountering a bear; it may be that areas indicated as low-quality may still have a high bear encounter rate that is only slightly lower than that of high-quality areas. Therefore these maps should be used only as guides to help managers make decisions to reduce human-bear conflict, and not as definitive visual references for avoiding bears.

Chapter 4

Why does the sheep cross the valley? Using unclassified spectral layers to explain bighorn sheep movements

4.1 Summary

As habitat availability in the southwestern United States declines, it is becoming more important to understand the habitat requirements of resident animal populations, particularly populations of desert bighorn sheep (*Ovis canadensis*). Ten individual bighorn sheep were captured and tagged within the Wonderland of Rocks and Queen Mountain region in Joshua Tree National Park to study the effectiveness of artificial water sources in maintaining their habitat (Longshore, Lowrey & Thompson 2009). It was observed that two individuals made routine trips to the nearby Pinto Range that did not have any documented permanent water, which is thought to be necessary for their survival. We hypothesized that differences in habitat availability, particularly the availability of moisture through plant succulence, allowed these individuals to travel freely between mountain ranges. Because traditional measures of vegetation cover can be inaccurate in desert environments, we accounted for differences in vegetation between the two mountain ranges by using unclassified spectral layers derived from satellite imagery, which were reduced via PCA into a single variable. We compared models of sheep movements within the primary mountain range and between both mountain ranges using AIC to identify differences in preferences between sheep that did and did not cross the valley. We then created habitat preference maps by projecting these preferences across the landscape to visualize any differences in perceived habitat quality between the

two groups of sheep. We found that differences in habitat preference were primarily in relation to vegetation and freestanding water. Sheep were found to select regions of higher vegetation when they did not have a relationship with freestanding water. In the east range, where there was no documented freestanding water, sheep preferred to move into and out of regions of high vegetation. Despite these differences, the projections of available high-quality habitat across the landscape were similar among all groups of sheep movement. Therefore, the Pinto Range may offer suitable habitat for all bighorn sheep and can be used to expand bighorn sheep habitat.

4.2 Introduction

Land use change in the southwestern United States has led to an increase in aridity, which is expected to continue to increase throughout the rest of the century (Jenerette & Wu 2001; Seager et al. 2007). These changes are caused by urbanization and agricultural expansion, which adds more fragmentation and complexity to a naturally fragmented landscape (Jenerette & Wu 2001; Scanlon et al. 2005; Grimm et al. 2008). This can lead to decreased precipitation, extended drought, and reduced soil moisture, which all change the distribution and composition of the vegetation (Jenerette & Wu 2001; Seager et al. 2007; Davies & Hall 2010; Munson et al. 2013). These impacts on desert habitat features can cause herbivores to change their behavior to meet water and foraging requirements (Brown, Valone & Curtin 1997; McKinney, Smith & DeVos Jr. 2006; Hoglander et al. 2015). Wildlife managers are concerned about the viability of many desert populations in the wake of these changes, particularly those of the desert bighorn sheep (*Ovis canadensis*) (Krausman 2000; Singer, Bleich & Gudorf 2000; Papouchis, Singer & Sloan 2001). Their populations are declining throughout the southwest, making it critical to

understand their resource requirements (Papouchis, Singer & Sloan 2001; Harris, Smythe & Henry 2009; Hoglander et al. 2015).

Bighorn sheep typically inhabit escape terrain, which include steep, rugged slopes that allow individuals to detect predators from large distances (Bailey 1980; Singer, Bleich & Gudorf 2000; McKinney, Boe & DeVos Jr. 2003). Suitable areas of escape terrain are widespread but only occur as islands within the higher elevation mountain ranges (Wehausen 2007). Therefore, populations are isolated between long stretches of unsuitable habitat on the desert floor (Bleich, Wehausen & Holl 1990; Singer, Bleich & Gudorf 2000). However, these seemingly isolated populations are connected by some individuals, usually rams, traversing the desert valleys between mountain ranges, which results in a metapopulation structure (Witham & Smith 1979; Hanski 1998; Wehausen 2007).

Bighorn sheep, particularly females, have been shown to be dependent on freestanding water (Blong & Pollard 1968; Turner 1970; Broyles 1995; Turner et al. 2004; Oehler et al. 2005; Dolan 2006; Sappington, Longshore & Thompson 2007; Wehausen 2007; Longshore, Lowrey & Thompson 2009; Bleich, Marshal & Andrew 2010). Models of bighorn sheep habitat have shown that the presence of freestanding water is an accurate predictor of sheep locations (Turner et al. 2004; Sappington, Longshore & Thompson 2007; Longshore, Lowrey & Thompson 2009; Bleich, Marshal & Andrew 2010). However, other studies have indicated that sheep can obtain enough succulence from vegetation alone and do not rely on freestanding water (Warrick & Krausman 1989; Krausman & Etchberger 1995; Broyles & Cutler 1999). The dependence of bighorn sheep populations on freestanding water likely varies with several factors,

such as climate, terrain, forage availability, and the presence of predators and competitors (Cutler 1996).

Joshua Tree National Park (JOTR), located in southern California, has had 12 permanent water guzzlers added to mitigate the loss of perennial water sources over time (Douglas 1975). Ten adult female bighorn sheep were captured and tagged within the Wonderland of Rocks and Queen Mountain region of the park to study the effectiveness of these artificial water sources in maintaining bighorn sheep habitat (Longshore, Lowrey & Thompson 2009). It was observed that two of these sheep made routine trips to the nearby Pinto Range that lacks any documented permanent water sources, which was unusual given that female bighorn sheep usually remain near freestanding water and rarely cross low elevation valleys (Witham & Smith 1979; Dolan 2006). The objective of this study was to compare the movements of the two groups of sheep to determine why some individuals crossed the valley between mountain ranges. We hypothesized that this behavior was caused by differences in habitat availability and/or differences in individual habitat preferences, particularly in regards to the availability of vegetation.

4.3 Methods

4.3.1 Study site

Our study took place within the northwestern portion of JOTR, California (34°N, 116°E; Fig. 4.1). In the Wonderland of Rocks and Queen Mountain region, elevation ranges from 680 m to 1775 m. Dominant vegetation consists of *Larrea tridentata*-*Ambrosia dumosa* associations at lower (<1000 m) elevations, *Yucca schidigera*, *Y. brevifolia*, and *Coleogyne ramosissima* associations at mid-elevations (900-1400 m), and *Juniperus*

californica associations at higher (>1100 m) elevations (Leary 1977). The Pinto Range reaches a maximum of 950 m. During our study, summer temperatures reached upwards of 47°C and winter temperatures were as low as -6°C. Average rainfall was approximately 13 cm/year, with two peaks occurring during the early spring and the late summer (temperature and precipitation data from Twentynine Palms [34° N, 116° W] National Climatic Data Center weather station). Sheep population size was estimated to be 54 individuals (95% C.I. 39-68) in 2003 and 59 individuals (95% C.I. 28-89) in 2004 (Thompson et al. 2007).

4.3.2 Location data

Sheep locations were provided by ARGOS satellite uplink capability collars (TGW-3580 store-on-board units, Telonics Inc., Mesa AZ). These collars were fitted to ten female adult bighorn sheep captured 29-30 October 2002 within the Wonderland of Rocks and Queen Mountain region of JOTR (Longshore, Lowrey & Thompson 2009). Location fixes were obtained three times daily (at 0500, 1200, and 2000 h) for each individual. We restricted our analysis to movements that ended within 1 km (33 pixels) of their starting locations, as this was considered a reasonable distance to travel between location fixes.

We labeled each movement as occurring within the “main” (Wonderland of Rocks/Queen Mountain) or the “east” (Pinto Range) region. We excluded the few movements that occurred within a smaller peak between the two primary mountain ranges. We separated the sheep data within the main mountain range between sheep that cross the valley at least once (transient) and those that do not (non-transient). To more accurately compare local habitat preferences, we only studied the five non-transient sheep that had overlapping ranges with the two transient sheep. We further divided all

movements into three seasons: spring (February – May), summer (June – September), and winter (October – January). Summer habitat is dependent upon the availability of permanent water sources, since this is when it is most limiting for bighorn sheep populations (Bleich, Bowyer & Wehausen 1997; Andrews, Bleich & August 1999; Turner et al. 2004; Sappington, Longshore & Thompson 2007; Longshore, Lowrey & Thompson 2009). Peak lambing season occurs during the spring months (Rubin, Boyce & Bleich 2000), which may influence the selection of habitat in comparison to the winter months. Transient sheep crossed the valley numerous times during the spring (21 crosses) and winter (18 crosses), but only infrequently during the summer (3 crosses).

4.3.3 Environmental data

We used elevation, slope (proportional scale from 0 to 1), ruggedness (Vector Ruggedness Measure ranging from 0 to 1; Sappington, Longshore & Thompson 2007), and distance from permanent water source (in km) as potential habitat predictors of sheep movement. Elevation was obtained from a digital elevation model, which was also used to calculate slope and the Vector Ruggedness Measure. This measure of ruggedness, which more effectively decouples terrain ruggedness from slope, was calculated with a script in ArcView using a 3 x 3 moving window (Sappington, Longshore & Thompson 2007). All habitat variables had a pixel size of 30 m by 30 m. We standardized each variable to have zero mean and unit standard deviation.

Vegetation is also an important component of sheep habitat (Krausman & Leopold 1986). Vegetation maps are commonly used as predictor variables to help determine available habitat for a species of interest (McDermid, Franklin & LeDrew 2005; Xie, Sha & Yu 2008). However, it is difficult to create traditional vegetation maps,

such as percent cover of a species of interest, in desert environments because of the relatively sparse vegetation in comparison to the dominance of the background soil (Smith et al. 1990). Alternative measures of vegetation such as the normalized difference vegetation index (NDVI) can also be affected by high relief, shadows, and the moisture content of the background soil (Huete & Jackson 1988; Kremer & Running 1993; Peters & Eve 1995; Sesnie et al. 2011; Yang, Weisberg & Bristow 2012). Instead, we used unclassified spectral images of the landscape as predictors of sheep movement. Images for each season were obtained from Landsat 4-5 TM and coincided with the dates of sheep movement. Images were processed in QGIS and exported to *Mathematica*. Principal Component Analysis (PCA) was performed on the six non-thermal spectral bands of each image to reduce the number of predictors while still maintaining most of the variation in the data. Only Principal Component 1 was used to represent vegetation further, as this layer captured more than 90% of the variation in each image. This variation is mostly in the short-wave IR1 spectral band, in which low reflectance is indicative of higher moisture content in the soil and vegetation (USGS 2013).

4.3.4 Fitting the model

We used conditional logistic regression to fit each movement i to different combinations of our k environmental layers. These layers inform the potential predictor values \mathbf{x}_j of every possible destination pixel j , which influence each movement. We included the distance between the current location and each potential destination pixel as an additional predictor to represent the cost of movement (Hjermann 2000). For each choice \mathbf{y}_j , the chosen pixel was assigned a value of 1 and 40 random pixels within a 33 pixel radius (density of 1 pixel per 78 km²) were assigned a value of 0. Under the conditional logistic

model, the probability p_j that an animal chooses a pixel j as the next location is

$$p_j = \frac{e^{x_j \beta}}{\sum_j e^{x_j \beta}} \quad [1]$$

where β is a k by 1 vector of parameters to be estimated. We took the logarithm of each chosen pixel p_j (where $y_j = 1$) to find the log-likelihood L_i of each movement, and we summed the L_i over all movements to find the log-likelihood of the entire movement path. We compared models of differing complexity using Akaike's Information Criterion (AIC). We calculated the importance of each parameter by summing the weights of the models in which the parameter appears.

4.3.5 Smoothing the environmental data

The spatial scale at which an organism responds to its surroundings may differ from the scale at which the data is measured (Holling 1992; Lima & Zollner 1996; Nams 2005; De Knecht et al. 2010; Marshall et al. 2011). Therefore, the spatial scale(s) chosen for study can be biologically irrelevant for the species in question (Levin 1992; Boyce 2006; Mayor et al. 2009; Wheatley & Johnson 2009; De Knecht et al. 2011). We implemented the smoothing process described in Mashintonio et al. (2014) to generate multiple spatial scales to identify the one(s) being used by the sheep. This was done for two variables: vegetation and ruggedness. Fig. 4.2 displays the vegetation layer at the original (unsmoothed) scale and smoothed with a 23-pixel radius kernel. These layers were overlaid with spring transient sheep movement segments to visually assess how individuals moved across this habitat. Smoothing the ruggedness layer is equivalent to creating a Vector Ruggedness Measure with a larger moving window and may more

accurately represent sheep preferences. The ‘distance to the nearest permanent water’ layer is intrinsically smooth.

To smooth these variables, we averaged each pixel with its neighboring pixels within an increasing radius, up to 66 pixels (~ 2 km, or twice the radius of available movement choices; Mashintonio et al. 2014). Due to the computational intensity of fitting 66 separate models for each dataset, along with the fact that individual scales of the same variable become more correlated at larger radii, we did not fit models at each individual radius; instead, we fit models at 13 different radii that increased logarithmically from 0. We included squared versions of each variable at each radius to allow for non-linear preference functions (Johnson et al. 2004; Johnson & Gillingham 2005; Mashintonio et al. 2014).

At each radius for each variable, we fit models using the original raster layer, the squared version of the raster layer, and both the linear and squared versions of the raster layer (Mashintonio et al. 2014). Each model also included the distance from current location parameter; furthermore, we included a distance-only model as a null comparison (Mashintonio et al. 2014). Models were compared using AIC. We chose candidate scales by looking for local minima in the AIC scores, but we inverted the y-axis so that optimal models would be shown as peaks (Mashintonio et al. 2014). These candidate scales were used as predictor variables, along with the other environmental layers, in the full model selection process.

4.3.6 Modeling sheep preferences

We first determined whether transient sheep and non-transient sheep have similar habitat preferences within the Wonderland of Rocks/Queen Mountain region. We used AIC to

compare models fit using transient and non-transient sheep movement data separately and combined. We summed the AIC scores of the best models for transient and non-transient sheep separately and compared it to the AIC score of the best model for combined sheep. A lower summed AIC score for the separately fit data indicates that the two groups of sheep should be modeled separately to capture differences in their preferences within this region.

Once it was determined that the transient sheep had different preferences than the non-transient sheep within the main range, we assessed whether the transient sheep themselves had different preferences when they inhabited different mountain ranges. We used the same predictor variables as above (for transient sheep) to fit models of all transient sheep movements, regardless of mountain range. For movements that occurred within the main mountain range, parameters were estimated using equation [1]. To identify whether these sheep displayed different preferences when moving in the east range, we estimated an additional “difference” parameter for each predictor variable such that the probability an animal chooses a pixel j as the next location is now

$$p_j = \frac{e^{x_j\beta + \beta Difference}}{\sum_j e^{x_j\beta + \beta Difference}} \quad [2].$$

Models included either the primary parameter only or both the primary and the difference parameters for each predictor variable. If the estimate of the difference parameter was small compared to the primary parameter, the preference for that habitat variable was considered similar across both mountain ranges. If it was large, however, and the difference parameter had a high measure of importance, individual sheep likely had different preferences for the same variable when in different mountain ranges. In this case, the parameter estimates for the sheep movements occurring only in the east range

were obtained by adding the difference parameter to the primary parameter; these were then compared to the parameter estimates for the sheep movements occurring only in the main range, which were obtained in the first analysis.

4.3.7 Preference maps

We used the parameter estimates for non-transient sheep movements and transient sheep movements in both mountain ranges to create habitat preference maps. These maps display the relative quality of each pixel given by $e^{x_j\beta}$. We first compared maps created using parameter estimates of transient and non-transient sheep in the main mountain range. These maps were overlaid with individual movement vectors to assess the map's ability to predict the quality of the habitat selected as well as to display the direction of sheep movement. We then projected the parameter estimates for each of these groups of sheep movement onto the east range and overlaid this projection with sheep movement end-points to assess how well they each predicted movements. We created additional maps using parameter estimates of the transient sheep in the east range to compare to the projected habitat quality. We also used these parameter estimates to project preferences back to the main range. For all maps, we visualized habitat quality within a 66-pixel radius of all sheep locations. We did not include the parameter estimate for water distance in these maps because it often had a large value that dominated the projection of pixel quality.

4.4 Results

4.4.1 Optimal spatial scales

Ruggedness. Both transient and non-transient sheep movements indicated a preference for the ruggedness layer at a scale greater than that of the original layer (30 m

cell size). Most sheep preferred ruggedness smoothed with a 3-pixel radius kernel (210 m cell size), including transient sheep in the spring and summer and non-transient sheep in the summer. In the winter, transient sheep selected ruggedness smoothed with a 1-pixel radius kernel (90 m cell size) and non-transient sheep selected ruggedness smoothed with a 6-pixel radius kernel (390 m cell size); non-transient sheep in the spring also selected ruggedness smoothed to 1 pixel. When the sheep movement data was combined, the optimal smoothing radius always coincided with that of the non-transient sheep movements, which were greater in number than the transient sheep movements.

Vegetation. Both transient and non-transient sheep movements in the spring had a relationship with the vegetation layer at two scales: the original layer (30 m cell size) and the layer smoothed with a 23-pixel radius kernel (1.41 km cell size; Fig. 4.3). In the summer, transient sheep movements maintained a relationship at two scales: the original layer and the layer smoothed with a 16-pixel radius kernel (990 m cell size; Fig. 4.3). Non-transient sheep movements only had a peak when smoothed to 1 pixel (Fig. 4.3). In the winter, both groups of sheep movements again responded to vegetation at two scales: the original layer and the layer smoothed to 16 pixels for transient sheep and 32 pixels for non-transient sheep (Fig. 4.3). The scales chosen for the combined data again matched those for the non-transient data.

In some cases, the curve of the AIC score continued to increase at large smoothing radii without peaking. We did not consider these scales to be ecologically important, since this result may be an artifact of the data. For instance, when smoothed at a very large scale, any movements towards or away from a slight environmental gradient

would be detected as selection for that variable at that scale, regardless of the reason for the movement (Mashintonio et al. 2014).

4.4.2 Same-location models

In all seasons, the ‘separate models’ AIC score was lower than the ‘combined models’ AIC score, demonstrating that it is better to model sheep movements separately (Table 4.1). This is in part due to the different spatial scales chosen for ruggedness and vegetation by the two groups of sheep, since only one of the scales was present in the combined dataset. In addition, some variables were important for both groups of sheep, but the relationships to that variable were different (e.g., slope; Fig. 4.4). Therefore, combining the sheep data precluded us from identifying opposing preferences for the same variable and different scales of selection.

4.4.3 Different-location models

In the spring, the importance value of every difference parameter was nearly identical to the corresponding primary parameter, even when neither parameter was important (Table 4.2). In the summer, the importance values of the difference parameters were always much lower than their corresponding primary parameters, particularly when the primary parameter had a high importance value (> 0.8 ; Table 4.2). The lower importance of the difference parameters in the summer was likely due to the small number of movements made in the east range during this season. In the winter, the importance values of the difference parameters were only slightly lower than their corresponding primary parameters, never by more than 0.02 (Table 4.2).

	Transient	Non-Transient	Total	Combined
Spring	3,652.33	13,301.58	16,953.91	16,991.1
Summer	3,651.12	11,527.22	15,178.34	17,017.9
Winter	2,965.56	11,991.80	14,957.36	15,001.1

Table 4.1. AIC scores for transient and non-transient sheep inhabiting the Wonderland of Rocks and Queen Mountain region in each season. Transient and non-transient sheep were modeled separately, and the sum of their AIC scores was compared to the AIC score of a model fit to the combined sheep data. In all cases, the ‘separate sheep’ AIC score (bold) was better than the ‘combined sheep’ score.

4.4.4 Sheep preferences

The shapes of the relationships for each of the predictor variables in the best model are shown in Fig. 4.4. These were derived using the parameter estimates of the important variables. All sheep in every season preferred higher elevations and rugged terrain, but some groups displayed a slightly hump-shaped relationship with ruggedness, where preference declined if the terrain was too rugged.

- **Spring.** Transient sheep preferred steep slopes in the main range but preferred intermediate slopes in the east range. Non-transient sheep avoided steep slopes. Transient sheep preferred locations that were close to permanent water while in the main range, but non-transient sheep did not consider distance from water important. Transient sheep in the main range also preferred regions of low vegetation, but in the east range they moved into and out of regions with high vegetation (u-shaped relationship). Non-transient sheep preferred regions of high vegetation.
- **Summer.** Non-transient sheep preferred steep slopes, but transient sheep did not consider slope important. Both transient and non-transient sheep moved into and

out of areas close to permanent water (u-shaped relationship). Transient sheep preferred intermediate amounts of local vegetation, while non-transient sheep preferred low and high amounts of local vegetation (u-shaped relationship).

- **Winter.** Transient sheep preferred steep slopes in the main range but avoided steep slopes in the east range. Non-transient sheep preferred intermediate slopes. Transient sheep kept a fixed distance (hump-shaped relationship) from permanent water in the main range, while non-transient sheep did not consider distance from water important. Transient sheep preferred a mosaic (hump-shaped relationship) of vegetation in the main range and again moved into and out of regions of high vegetation in the east range. Non-transient sheep selected small patches of low vegetation within regions of high vegetation.

4.4.5 Habitat preference maps

Although there were differences in parameter estimates between transient and non-transient sheep in the main mountain range, the habitat preference maps predicted similar high-quality areas in all seasons (Fig. 4.5, main range). However, during the summer and fall, the high-quality areas are more extensive for transient sheep than non-transient sheep. Despite this, the projection of habitat quality in the east range is nearly identical for all datasets (Fig. 4.5, east range). None of these projections predict the southern portion of habitat along the ridge to be high quality despite several sheep movements in this area. Preference maps created using east-range movements did identify this area as being high quality in addition to extending the other high-quality areas (Fig. 4.6, east range). When applied to the main range, even more habitat is projected to be high quality (Fig. 4.6, main range).

	Spring	Summer	Winter
Elevation (difference)	1.0 (1.0)	1.0 (0.56)	1.0 (0.98)
Elevation Sq (difference)	0.51 (0.51)	0.99 (0.56)	1.0 (0.98)
Slope (difference)	0.98 (0.98)	0.37 (0.23)	0.14 (0.14)
Slope Sq (difference)	0.82 (0.82)	0.23 (0.09)	0.56 (0.55)
Ruggedness (difference)	1.0 (1.0)	1.0 (0.56)	1.0 (0.98)
Ruggedness Sq (difference)	1.0 (1.0)	1.0 (0.56)	0.98 (0.96)
Water Distance (difference)*	0.71 (-----)	0.89 (-----)	0.94 (-----)
Water Distance Sq (difference)*	0.68 (-----)	0.87 (-----)	0.94 (-----)
Vegetation- local (difference)	0.57 (0.57)	0.22 (0.08)	0.20 (0.19)
Vegetation- local Sq (difference)	0.40 (0.40)	0.93 (0.52)	0.31 (0.30)
Vegetation- regional (difference)	0.65 (0.65)	0.19 (0.08)	0.41 (0.40)
Vegetation- regional Sq (difference)	0.99 (0.99)	0.24 (0.12)	0.99 (0.97)

*Importance values calculated using parameter estimates of main-range only transient sheep movements.

Table 4.2. Importance values for parameter estimates of transient sheep movements in each season. The importance of the primary parameters was determined using all transient sheep movements; the importance of the difference parameters was determined using only the transient movements in the east range. Variables with importance values greater than 0.8 (bold) are considered important for determining sheep movements.

4.5 Discussion

The transient sheep that inhabit the Wonderland of Rocks and Queen Mountain region of JOTR have slightly different habitat preferences than the non-transient sheep that inhabit the same area. The transient sheep also select different habitat when they leave the main mountain range and travel to the Pinto Range. The different availability of certain habitat in the Pinto Range is likely due to the lower elevation and the resulting changes in vegetation composition, which was captured in our PC1 layer. This layer is primarily composed of the short-wave IR1 spectral band, which discriminates the moisture content of the soil and vegetation, so it is possible that these transient sheep are able to obtain water from other sources when in the Pinto Range.

The importance of freestanding water to bighorn sheep populations likely varies with several factors, including season, climate, terrain, forage availability, and the presence of predators and competitors (Cutler 1996). Freestanding water is most limiting during the dry summer months (Turner 1970; Campbell & Remington 1979; Broyles 1995; Bleich, Bowyer & Wehausen 1997; Andrews, Bleich & August 1999; Turner et al. 2004; Oehler et al. 2005; Sappington, Longshore & Thompson 2007), which explains why most movements between the two mountain ranges occur during the spring and winter. During the summer, both transient and non-transient sheep move in and out of areas near permanent water. This may be to avoid competition for use of the water guzzlers (Boyce et al. 2003; Ostermann-Kelm et al. 2008; Whiting et al. 2011; Simpson, Stewart & Bleich 2011) or to avoid predators that may hunt opportunistically near permanent water sources (Rosenstock, Ballard & DeVos Jr. 1999; DeStefano, Schmidt & DeVos Jr. 2000; Simpson, Stewart & Bleich 2011). During the other seasons, non-transient sheep do not have a preference for water distance but select large-scale regions of vegetation (Fig. 4.4). Transient sheep have similar relationships between water distance and regional vegetation in each of the other seasons: during the spring, they prefer short distances to water and low vegetation, whereas during the winter, they maintain a fixed, intermediate distance from water and prefer an intermediate amount of vegetation. When transient sheep were in the Pinto Range and far from permanent water, they avoided the edges of large regions of vegetation, instead preferring to be either outside this area or within. This relationship is evident in their movement patterns in the Pinto Range, where smoothed vegetation is found as a ring around the peak of the mountain (Fig. 4.2, bottom). Individuals are usually found within this ring, but otherwise

are at higher elevations with lower amounts of vegetation. They may behave this way because too much vegetation cover can inhibit the sheep's ability to detect approaching predators, but it also allows individuals to fulfill their water requirements when there are no nearby sources of freestanding water (McCutchen 1981; Risenhoover & Bailey 1985; Warrick & Krausman 1989; Krausman & Etchberger 1995; Sesnie et al. 2011; Harkleroad & Krausman 2014).

The use of difference parameters revealed that the transient sheep themselves have different preferences in each of the mountain ranges. This indicates that there are no inherent habitat preferences of some individual sheep that cause their attraction to the east range. Moreover, the projections of the preferences of transient and non-transient sheep movements in the main range to the east range both predicted the presence of high-quality habitat. Therefore, there is suitable habitat for both groups of sheep in the east range despite their differing preferences, and it is not unusual for some individuals to travel to this range. Maps of the east range made using east-only movements revealed more extensive high-quality habitat, both in the east range and when projected to the main range. Therefore, when in the east range, sheep appear to have a broader range of suitable habitat.

Habitat preference maps created using the parameters of all transient movement data closely mirrored the maps created using only the main-range transient movements (not shown). The prediction of habitat quality in the east range was therefore more similar to the projected quality (Fig. 4.5) than the actual quality (Fig. 4.6). This is because only a small subset of all transient movements occurred in the east range, the removal of which was not enough to cause a drastic change in the parameter estimates between the

main-range movements and all movements. This pattern was also true for comparisons between the transient and non-transient sheep movements in the main range, the latter of which comprised the majority of the combined sheep movements. This highlights the fact that there are differences in habitat preference among individuals, and that combining movement data from multiple individuals can mask this variation. Maps created using parameters for the full dataset can fail to identify the full extent of high-quality habitat. There are certainly differences in habitat preferences among the five non-transient sheep used in this study, but we expect these differences to be smaller than the differences between all non-transient sheep and the transient sheep. Likewise, the preferences identified by transient sheep movements in the east range would be overlooked without the use of difference parameters, but these movements occur within a separate mountain range with different habitat availability and thus were expected to differ from movements in the main range.

The smoothing analysis indicated that bighorn sheep had a relationship with the vegetation layer at multiple spatial scales, even though the final models for all but one dataset ultimately included vegetation at only a single spatial scale. Each analysis included a peak at a local scale, usually the original 30 m raster layer, and at a regional scale. This regional scale was consistent for all sheep during the spring (23 pixel radius kernel) and all transient sheep in the summer and fall (16 pixel radius kernel). Additionally, the optimal scale for ruggedness was always larger than the original raster layer, indicating that the window size we used for the VRM was not large enough. This layer was consistently selected at a one- or three-pixel radius kernel in all but one dataset, indicating an inherent scale of selection for this species in a particular environment. The

consistent peaks at these specific smoothing radii may have been the result of only using a few selected radii instead of the full continuum, which was not computationally feasible with the size of each pixel (30 m) and the maximum radius (66 pixels). Nevertheless, we show that habitat preferences are better evaluated by including environmental information at multiple spatial scales (Bowyer & Kie 2006; Mayor et al. 2009; Mashintonio et al. 2014).

In this study we used unclassified spectral layers to represent vegetation. To have a manageable number of predictor variables, we reduced the six spectral bands to one principal component, which captured more than 90% of the variability in the bands. Although this makes it harder to interpret the characteristics of the landscape to which sheep are responding, we have shown that bighorn sheep do in fact respond to this layer at varying spatial scales. Further analyses on the individual spectral bands and ground-truth surveys will help to identify more specific landscape features that the sheep are responding to.

Individual bighorn sheep may cross the valley into the Pinto Range for several reasons beyond inherent differences in the quality of the habitat or major differences in habitat preferences. The Pinto Range has more of this vegetation variable, likely making it possible for individuals to travel far from freestanding, permanent water. According to the habitat preference maps, all non-transient sheep included in this study would also find high-quality habitat within the Pinto Range, so there is no inherent biological reason why these individuals do not cross. The frequency of the trips made by the transient sheep indicates that the valley may not be particularly difficult to cross. Their attraction to the Pinto Range may have more to do with the lack of predators and competitors for water.

We did not have access to mountain lion movement data, but the Pinto Range may represent a haven from predators that live near the Wonderland of Rocks/Queen Mountain region. Because of the decline in available habitat for bighorn sheep throughout the southwestern US, particularly in JOTR (Longshore, Lowrey & Thompson 2009), these findings may represent an opportunity to expand the range of bighorn sheep that inhabit this region.

Chapter 5

Conclusions

Individuals of different species interact with each other and their environment in different ways, making it difficult to implement a single modeling framework for all species. This dissertation explored these differences in habitat selection as it relates to spatial scale in three distinct ecological systems. It is evident that for all three species under study – savannah elephants, brown bears, and desert bighorn sheep – the spatial context of the environment matters to individuals and can alter what we know about their habitat requirements.

Because of differences in the structure of the landscapes and the behavior of the species, smoothed environmental data were incorporated into models of habitat selection in different ways for each system. When all individuals within a group are expected to have similar habitat preferences and the number of predictor variables requiring smoothing is small, model fitting and selection can be done for all combinations of variables. This was the approach taken for the elephant data. Although the number of predictors was also small for the bighorn sheep data, individuals were expected to have different preferences within different mountain ranges. We still were able to fit all combinations of variables but included a difference parameter for each predictor variable, which allowed us to determine if there were any differences in preference. Finally, because of the complexity of the Kenai Peninsula, smoothing the environmental variables resulted in too many predictor variables to fit all models of bear preference. For this situation, we determined a relative ranking of the variables to fit specific combinations.

When individuals roam widely throughout a landscape they all face similar habitat choices. Therefore, movements of individuals with similar characteristics, such as age, sex, or season of movement, can provide an accurate measure of selection when combined. We expected elephants to have different habitat preferences between males and females and between the wet and dry seasons, but individuals within these groupings likely have similar preferences. Alternatively, individuals maintaining small ranges that cover only a small portion of the landscape may display vastly different habitat preferences if the available habitat differs for each of them. This was the case for the Kenai Peninsula, in which bears inhabit both the high-elevation mountains as well as the glaciated lowlands. This division in the landscape means that the habitat available to bears in the highlands, such as alder and willow, is not always available to bears in the lowlands, and thus these movements must be analyzed separately. We partially accounted for this by clustering the landscape into regions of similar habitat makeup and combining bear movements within each region. These clusters were created using the environmental layers smoothed with a 10-pixel radius kernel, which resulted in a coarsely heterogeneous landscape structure. Individuals within each region are thus faced with more similar habitat choices than individuals in different regions. Within each region, however, there are still local neighborhoods of finely heterogeneous habitat that may be different from other neighborhoods elsewhere in the region, leading to different preferences between individuals. These different scales of landscape heterogeneity are directly related to the scales at which individuals make habitat choices. Assessing habitat selection across a range of spatial scales thus allows us to identify the degree to which individuals perceive landscape heterogeneity.

Although the structure of the landscape can influence the habitat chosen by individuals, there may also be inherent individual variation in habitat preferences. This has been incorporated into models of habitat selection through the use of random coefficients, which are applied to the parameter estimates in the logistic regression equation (Gillies et al. 2006). However, this term can only be applied to a single variable in an RSF at a time, which precluded its use in our bear analysis (Gillies et al. 2006; Duchesne, Fortin & Courbin 2010; Roever, Van Aarde & Leggett 2012). Individual habitat preferences have been modeled separately (Roever, Van Aarde & Leggett 2012), but after separating each individual's movement by season and region, some datasets were too small to further subdivide by individual. This would also make it more difficult to interpret regional trends in habitat quality, especially since each individual could perceive a particular habitat variable at slightly different spatial scales. Therefore, our predictions represent the habitat quality for the average individual bear and not necessarily the best habitat for every bear.

The behavioral differences between our two groups of sheep – those that crossed the valley between the mountain ranges and those that did not – indicated the possibility of inherent differences in habitat preferences because all individuals had equal access to the entire landscape. Although there was enough movement data for each individual to be analyzed separately, we did not expect there to be noteworthy differences in their preferences within the behavioral groups. One approach for testing this could be to analyze the variation between individuals' differing preferences within each group and compare it between groups. This would reveal whether individuals within each group have more similar preferences compared to individuals in the other group.

Despite the differences in the structure of the landscapes and the behavior of the organisms, there were some similarities between all three studies. The parameter describing the distance from an individual's current location was consistently negative for all three species, implying that organisms prefer locations that are close over those that are far. Both elephants and bears had a similar range of parameter estimates: -0.97 to -1.39 for elephants and -0.94 to -1.43 for bears. The probability of movement was highest for a distance of 0.5 km, or 1 pixel, and ranged from 0.36 to 0.44. The parameter estimates for bighorn sheep were much closer to zero, ranging from -0.14 to -0.19, which indicates that the distance to the chosen location has a lesser influence on sheep movements. However, the maximum distance of any sheep movement was restricted to < 1 km, and the probability of moving was highest for distances of 270 m (for -0.14) and 180 m (for -0.19). Sheep therefore moved even *less* than elephants or bears despite the smaller parameter estimates. This discrepancy between sheep and the other species is likely due to the size of the pixels for the sheep data (30 m vs. 500 m). This smaller pixel size allows sheep to choose locations that are more pixels away from their current locations compared to elephants and bears, even though this is a smaller distance within the landscape. This resulted in the lower parameter estimate for sheep because the distance parameter is evaluated in pixels, not meters. It is possible that more fine-scale environmental information for elephants and bears would reveal a higher preference for moving distances even less than the 0.5 km indicated here. Nevertheless, it is evident that all three species prefer shorter local movements.

In each study, spatial scales larger than that of the original data were identified as important for animal movement. For most datasets, different habitat variables were

important at different scales, and some variables were important at multiple scales. The scales that were selected formed patterns for some groups of organisms. For example, elephants appeared to select most habitat variables at smaller scales in the dry season compared to the wet season, when individuals are not restricted in their movements to locations near water. All sheep groups (with one exception) were consistent in their patterns of selection for smoothed habitat variables: a single, small scale for ruggedness and both a small and large scale for vegetation. Alternatively, bears selected habitat across a wide range of spatial scales with little consistency between regions and seasons. This is likely due to the solitary nature of bears and the complexity of their landscape. Individual bears and elephants selected habitat at scales as large as 9.5 km and 10 km, respectively, and as small as 500 m (base scale). This scale may even be too coarse for some variables, as evidenced by the hump-shaped relationship that individuals had with these variables. Sheep had a much smaller maximum chosen scale of 960 m, which coincides with their smaller choice radius of movements (1 km). They also selected habitat at the base scale, which in this case is 30 m.

These differences highlight the fact that different organisms respond to their environments at different scales, and that a single resolution of environment data may not be appropriate for all species. In addition, these species all integrate aspects of their environment across multiple spatial scales, further stressing the importance of smoothing the environmental data to find the optimal scales. Researchers who analyze preferences across too few scales risk missing the true scales at which individuals select habitat (Jackson & Fahrig 2014). This can be problematic for determining high-quality habitat across large regions and can lead to incorrect assumptions about habitat preferences.

Recent studies have begun to assess selection across multiple spatial scales and have identified important scales for different species (e.g. De Knecht et al. 2010; De Knecht et al. 2011; Fisher et al. 2011). Understanding the correct scales at which threatened species perceive their surroundings can lead to better conservation and management.

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Appendix A

List of Figures

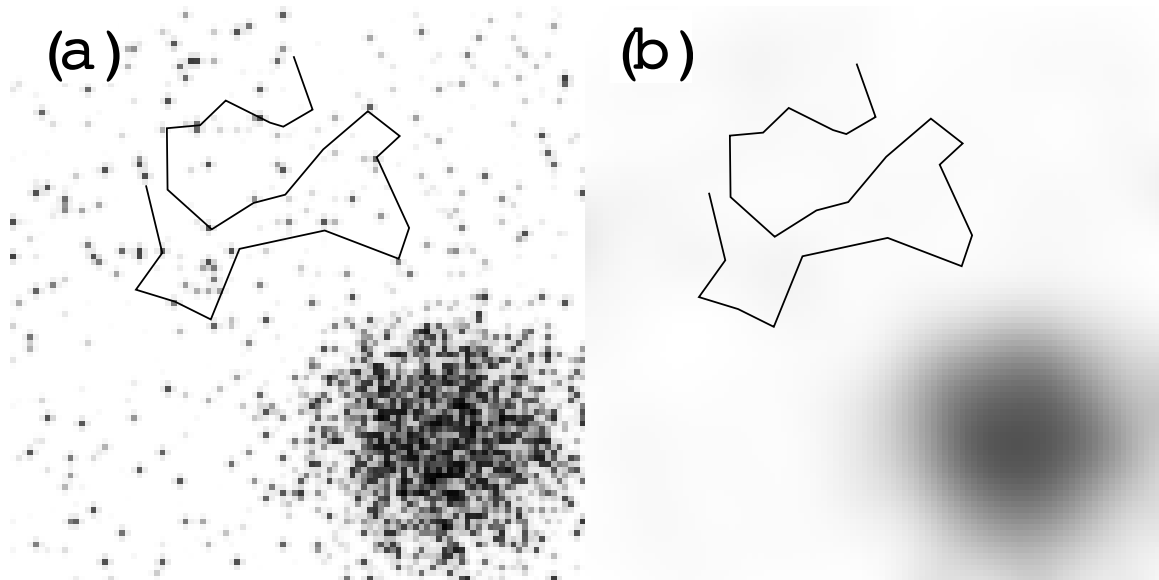


Figure 2.1. Example of how spatial scale can affect preference. (a) Hypothetical store density map of a city and surrounding suburbs, where dark grid squares represent high store density, overlaid with the movement path of a suburban family. Local movements indicate a preference for stores, but this preference does not extend to the city, where shopping opportunities are abundant. (b) Store density map after smoothing with a 21-pixel Gaussian filter. Now, it is apparent that the family selects against store density at a larger scale, even though it selects for store density at a smaller scale.



























Pattern	Small-scale preference	Medium-scale preference	Large-scale preference	Interpretation
A				Likes x at all scales
B				Likes small clearings in x
C				Likes medium clearings in x
D	 or 			Likes a mosaic of x (not necessarily x itself)
E	 or 			Likes the edge of x (not necessarily x itself)
F				Likes medium clumps of x
G				Likes small clumps of x
H				Doesn't like x at any scale
I				Smallest data scale is too coarse
J	 or 			Avoids edges of x
K		N/A	N/A	Moves in and out (point or linear feature)
L		N/A	N/A	Keeps a fixed distance (point or linear feature)

Figure 2.2. Possible interpretations of certain combinations of selection functions at small, medium, and large scales. Small-scale refers to smoothing <5 pixels, medium-scale refers to smoothing up to the choice radius (10 pixels), and large-scale refers to smoothing greater than the choice radius. Point and linear features are coded as ‘distance to...’ arrays, which are intrinsically smooth at scales up to the typical distance between features, and so are analyzed without further smoothing.

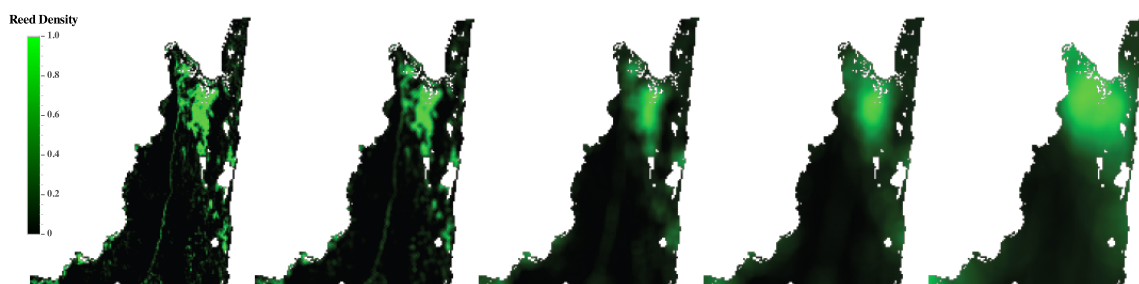


Figure 2.3. Proportion of reeds in Maputo smoothed at increasing scales. The original (base-scale) landscape is on the left, followed by landscapes smoothed at 1, 5, 10, and 20 pixels.

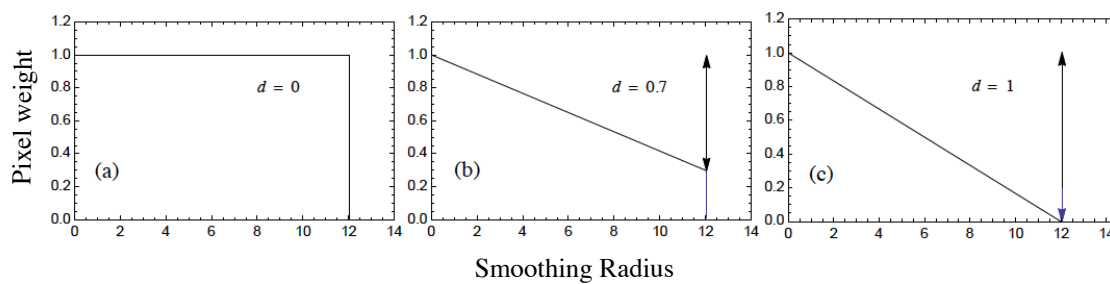


Figure 2.4. Smoothing kernels with varying decay. (a) A flat smoothing kernel, where all pixels within the radius are averaged equally. (b-c) Decaying smoothing kernels, where pixels closest to the central pixel are weighted more heavily in the average than pixels that are farther away.

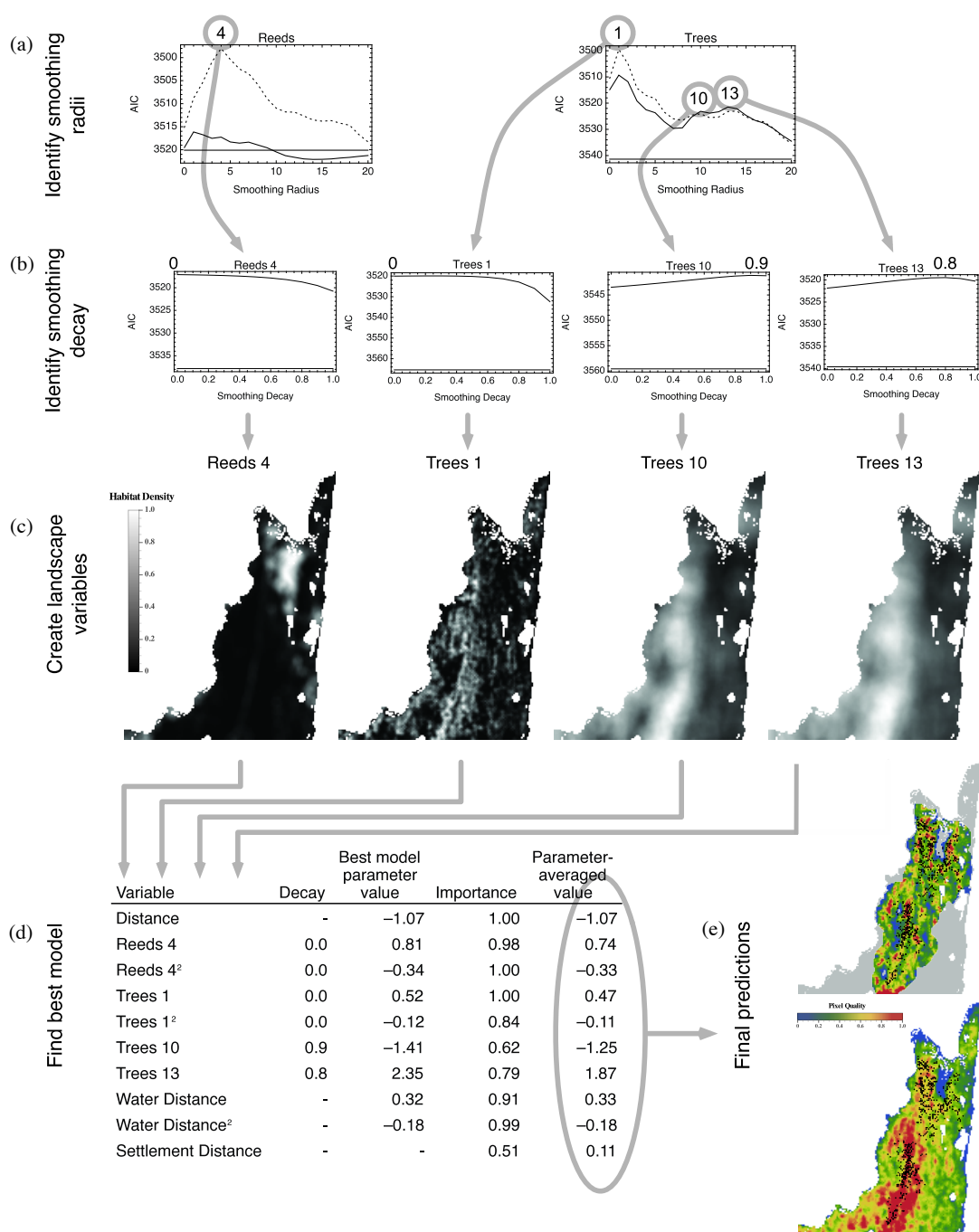


Figure 2.5. Process of model selection with multiple scales. (a) Identify smoothing radii.

The smoothing radii for the variables ‘reeds’ and ‘tree cover’ were optimized separately

for three models: ‘distance from current location’ only (flat solid line), distance and

habitat variable (jagged solid line), and distance with both the linear and quadratic variables (dashed line). Each of the peaks of model fit at the various radii is indicated. (b) Identify smoothing decay. The decay was optimized for each of the optimal radii in (a). The optimal decay for each radius is indicated. (c) Create landscape variables. Maps were created for each of the variables at the optimal radius and decay. Each map is a composite of the linear and quadratic values. (d) Find best model. The overall model choice uses ‘distance from current location’, each of the selected variables at the optimal radius and decay, ‘distance to water’, and ‘distance to human settlement’ (if applicable) as input parameters. The best model was chosen as the combination of model parameters with the lowest AIC score; in this case, the score was 3,472.33. The importance of the parameter is measured from the weights of the models in which it appears, and the parameter-averaged value is the value of the parameter averaged across all models. (e) Final predictions. The local relative quality map was created using the parameter-averaged values for all of the model parameters and applied to the 10-pixel radius of local movement choices for each start point (top). The map was overlaid with the endpoint of each movement to assess elephant choice. The landscape-wide relative quality map was created using the parameter-averaged values for all of the model parameters and applied to the entire landscape (bottom). The map was overlaid with the endpoint of each movement to assess elephant choice.

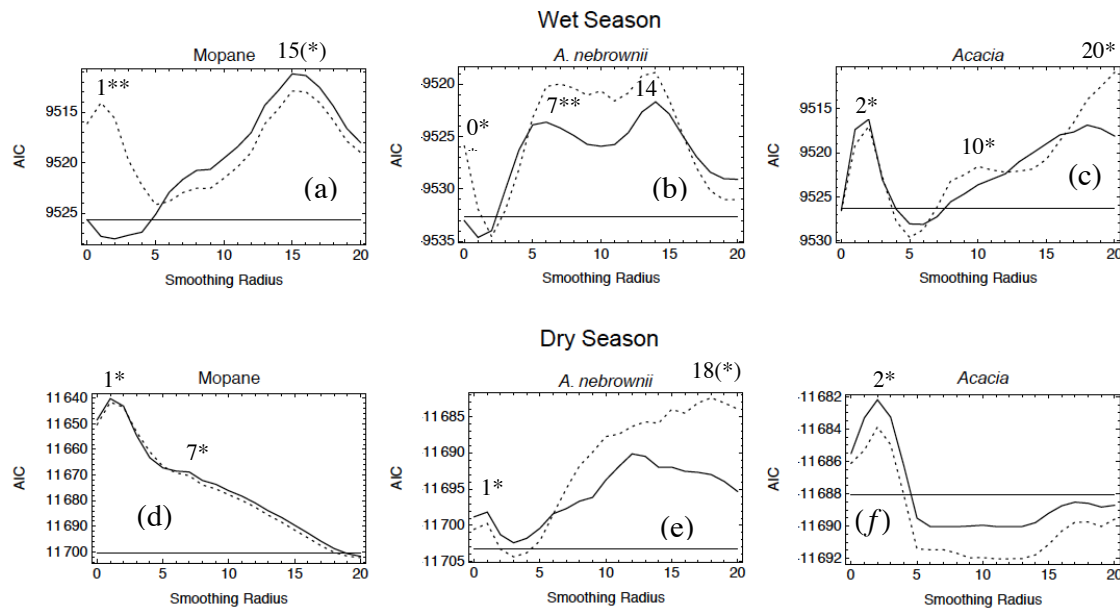
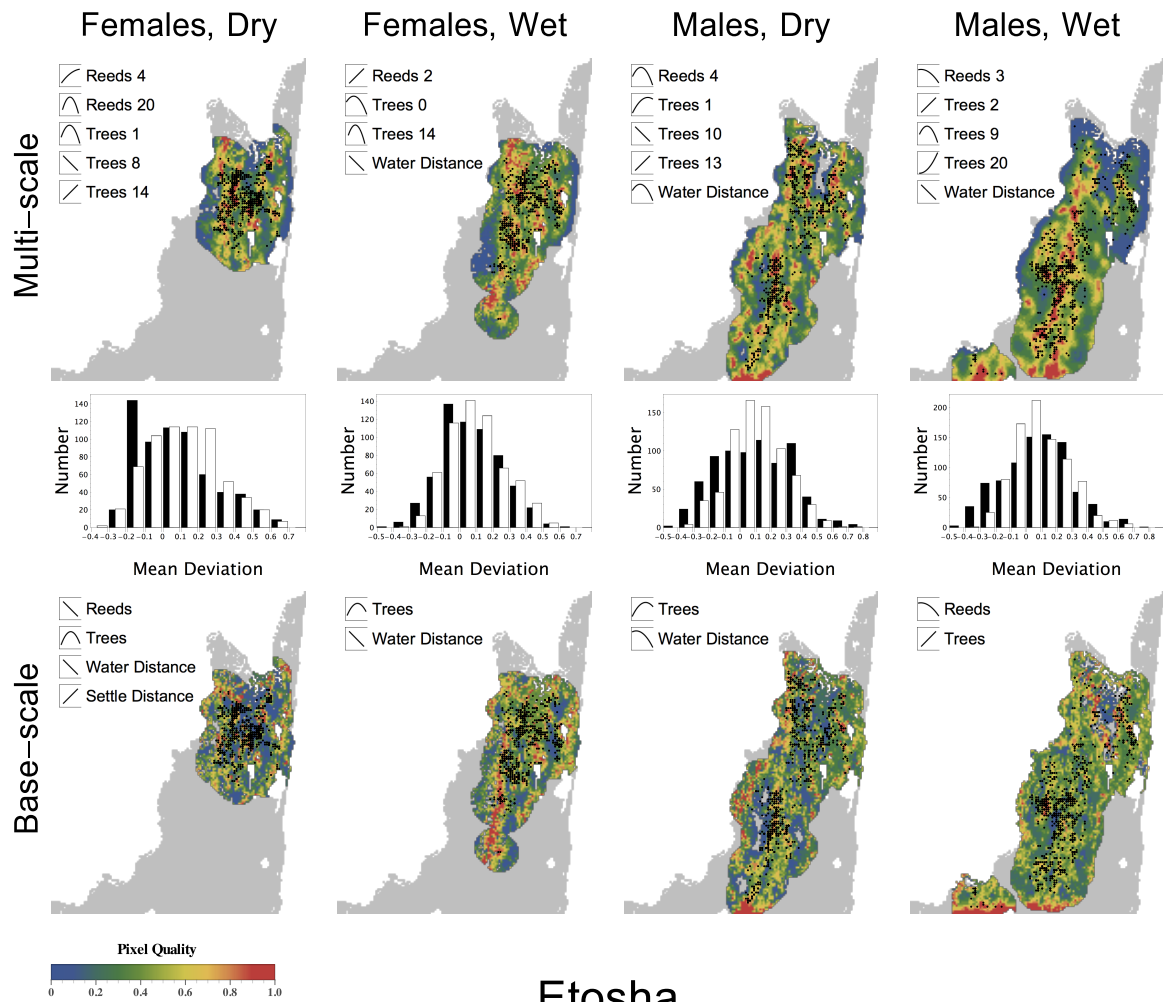


Figure 2.6. Habitat selection by female elephants in Etosha for the variables ‘mopane’, ‘*A. nebrownii*’, and ‘*Acacia*’ in both the wet and dry seasons. (a-c) During the wet season, when water is not limiting, individuals utilize more of the landscape and select habitat variables at larger scales more strongly than in the dry season. (d-f) During the dry season, when individuals are more restricted in their movements to areas near water, habitat variables are typically selected more strongly at a smaller scale than at a larger scale. Each variable is fit to three models: ‘distance from current location’ only (straight solid line), distance and the linear habitat variable (jagged solid line), and distance with both the linear and quadratic values (dashed line). Each of the peaks of model fit is indicated. A single asterisk indicates that only the linear value was chosen, and a double asterisk indicates that both the linear and quadratic values were chosen. An asterisk in parentheses indicates that the variable was not included in the best overall model.

Maputo



Etosha

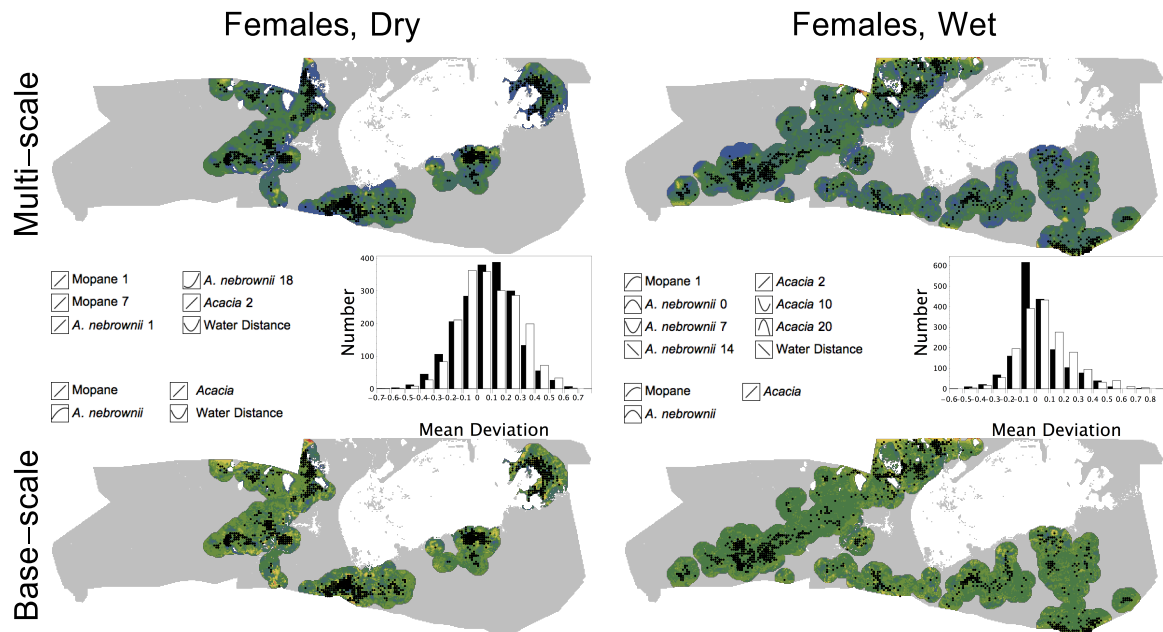


Figure 2.7. Local relative quality maps. The maps were overlaid with the endpoint of each movement for all elephant datasets, representing the composite of all variables present in the best multi-scale model and the original, base-scale variables only. The histograms show the comparison between the mean deviation of the probability values of the multi-scale maps (white) and base-scale maps (black). The variables at their optimal scale(s) are shown with the shape of the elephant's relationship to each variable.

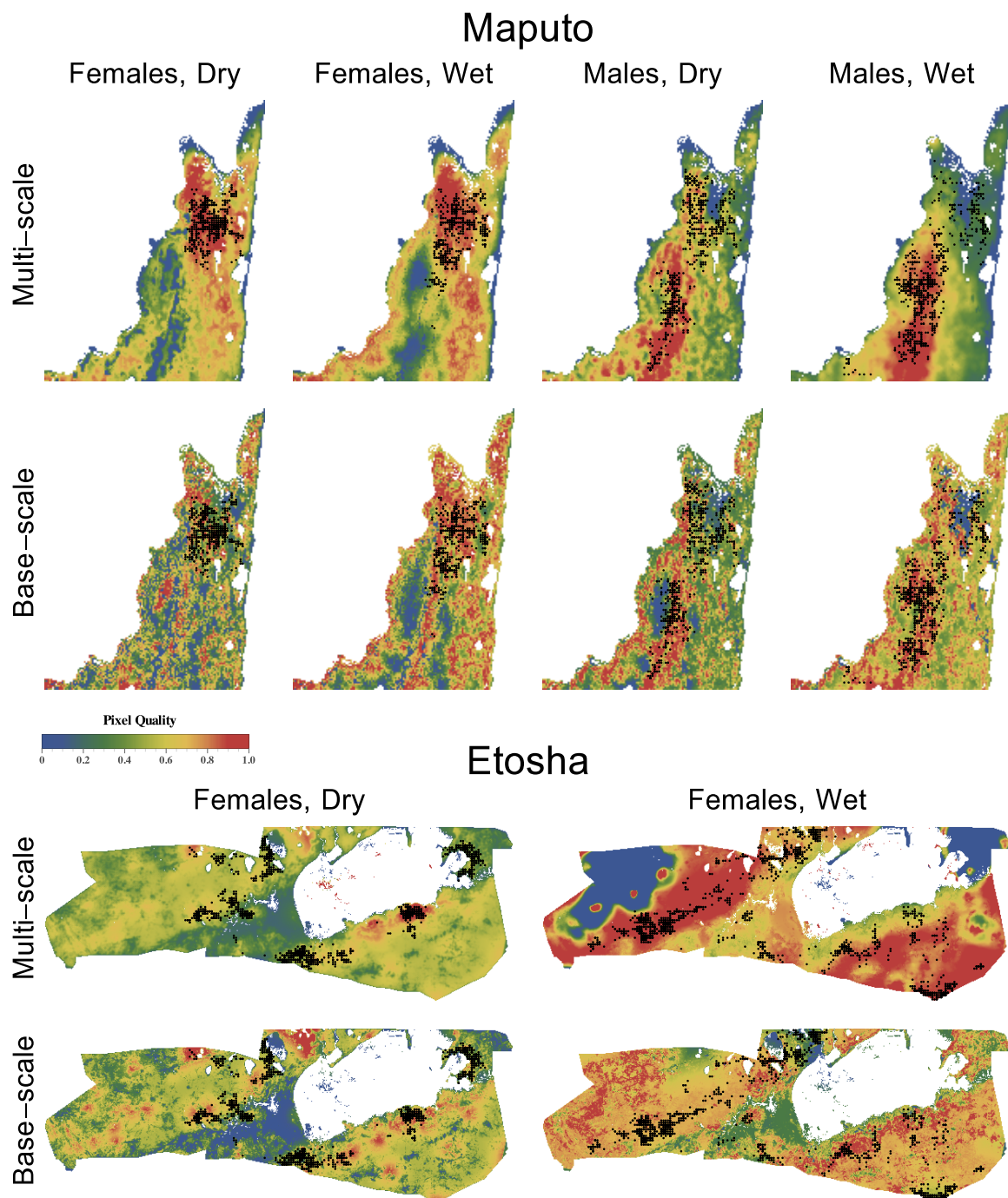


Figure 2.8. Landscape-wide relative quality maps. The maps were overlaid with the endpoint of each movement for all elephant datasets, representing the composite of all variables present in the best multi-scale model and the original, base-scale variables only.

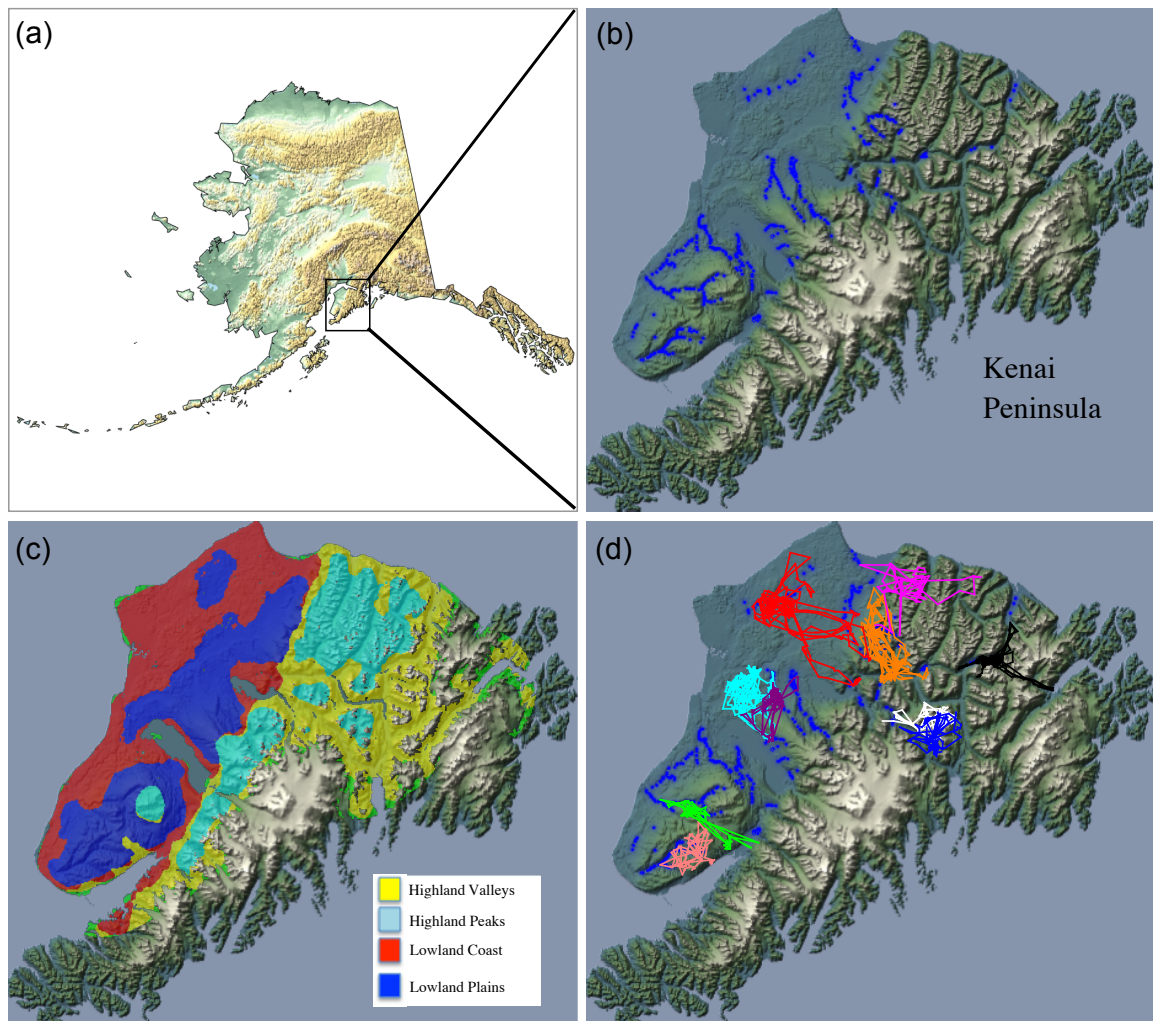


Figure 3.1. (a) Outline of the state of Alaska, indicating the position of the Kenai Peninsula. (b) Map of the Kenai Peninsula. The eastern two-thirds is dominated by the high elevation Kenai Mountain Range, and the western one-third is a glaciated plain with numerous lakes and streams. Blue areas represent stream locations that were frequently visited by brown bears. (c) Clusters that the landscape was partitioned into based on the makeup on the habitat. The four primary clusters are labeled; the fifth cluster (green coloring) included pixels that did not fit well into any of the other four clusters and thus was not used for the analysis. (d) Movement paths of a group of collared bears during

1997. For the most part, each individual occupies a different area of the landscape and does not overlap much with neighboring individuals.

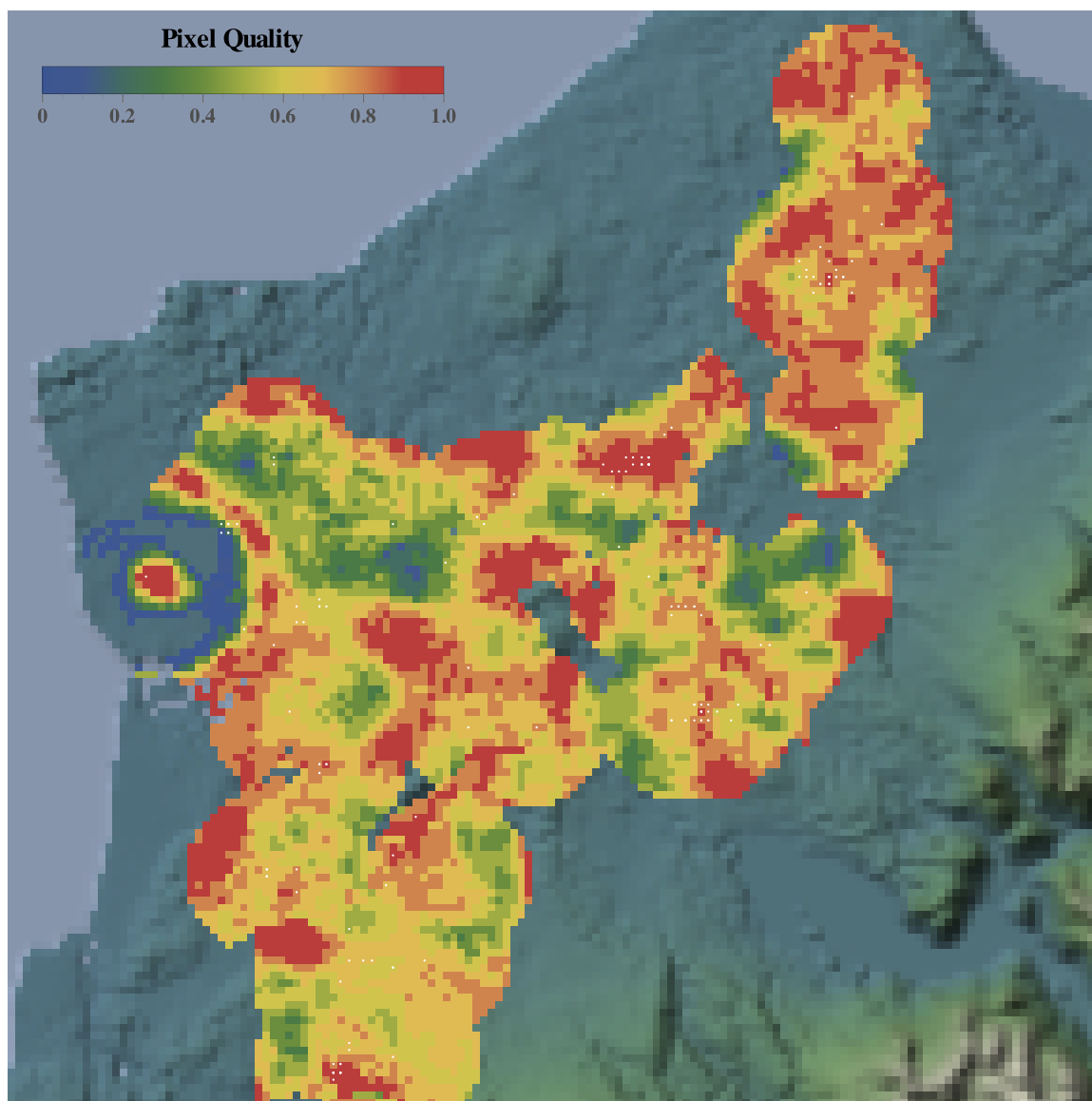


Figure 3.2. Sample relative local quality habitat preference map, overlaid with the endpoint of each movement in the lowlands regions during the summer. The map was created using the parameter estimates from the best model applied to a 10-pixel radius surrounding each movement start point. Each pixel is scaled from blue (low quality) to red (high quality). Chosen locations are more often in high-quality pixels than low-quality pixels.

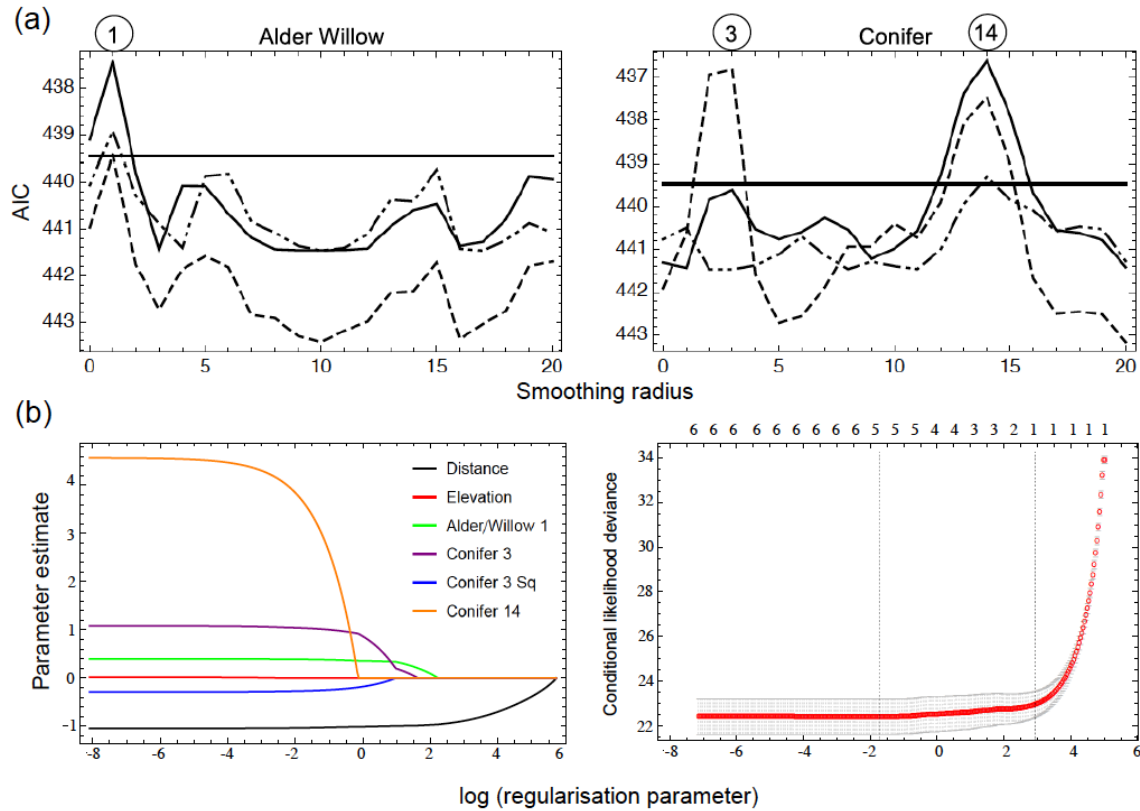



































































































































Figure 3.3. Process of model selection for a reduced dataset, used for illustrative purposes. (a) Optimization of the smoothing radius. Each of the seven vegetation variables (alder/willow, alpine, conifer, deciduous, mixed forest, spruce, and wetland) was smoothed independently to discover the optimal scale(s). Four models were fit at each radius: distance from current location only (flat solid line), distance and vegetation variable (jagged solid line), distance and vegetation variable squared (dotted/dashed line), and distance with both the linear and squared vegetation variable (dashed line). The chosen scales are indicated above the peaks. Each chosen scale was further optimized to find the appropriate level of drop-off of the smoothing kernel, or *decay* (not shown). (b) Parameter estimation and cross-validation using conditional logistic regression with lasso penalties, which uses each of the vegetation variables at their chosen scales from (a), ‘distance from current location’, and elevation as input parameters. ‘Distance from

nearest neighbor' was later included as an additional parameter. At the lowest value of the regularization parameter λ , all variables are in the model (left). As λ increases, the parameter estimates shrink towards zero. The variables that shrink first are less important to the model than those that shrink later. In this example, 'distance from current location' would be the most important variable, followed by alder/willow 1, conifer 3, conifer 3 squared, conifer 14, and finally elevation. Cross validation was initially used to determine the optimal model (right). The leftmost vertical line is at the λ where deviance is minimized, and the other is at the λ one standard deviation away from the minimum. In this example, the best model would have five parameters if the minimum deviance is used but only one parameter- 'distance from current location'- if the minimum plus one standard deviation is used.

Dataset	Elevation	Alder/ Willow	Alpine	Conifer	Deciduous	Mixed Forest	Spruce	Wetland	Neighbor distance	$\Delta AICc$
Spring, Highland Valleys		1 	4  8 	3  14 	2 	1 	—	0 	—	0.2
Summer, Highland Valleys		1  12 	1  5  10 	6 	1 	1 	3 	3 		-19.4
Fall, Highland Valleys		4  12 	0  11 	4 	—	5 	2 	0  2 		-20.4
Spring, Highland Peaks		5 	15 	3 	0  3 	0  2  12 	9 	9 		-5.0
Summer, Highland Peaks		0  3  6 	2  11 	3  12 	0  13 	0  16 	3  9  12 	0  7  13 		-8.2
Fall, Highland Peaks		2 	0  14 	1  10 	3  9 	9  13 	2  11 	2  6 		-5.7
Spring, Lowland Coast		10 	—	4 	1  4 	2  5 	0 	0 	—	0.7
Summer, Lowland Coast	—	4 	6 	6 	0  13 	2  19 	6  15 	0  4 	—	1.0
Fall, Lowland Coast		3 	4 	2  6 	3  5  16 	4  10  15 	4  14  19 	5  13 		-1.5
Spring, Lowland Plains	—	6 	—	1 	—	7 	8 	0 	—	3.0
Summer, Lowland Plains		—	—	—	—	4 	1 	—	—	2.0
Fall, Lowland Plains	—	1 	—	—	0  5 	—	9 	0  3 	—	N/A*

*Not enough movements had neighbors to fit a model.

Figure 3.4. The important predictor variables and their functional shapes for each data set. For variables that were smoothed, the optimal scale (radius of smoothing kernel) is indicated. Distance from current location was present and negative in all data sets (not

shown). ΔAIC measures the difference in AIC score between the best model with and without the neighbor distance parameter.

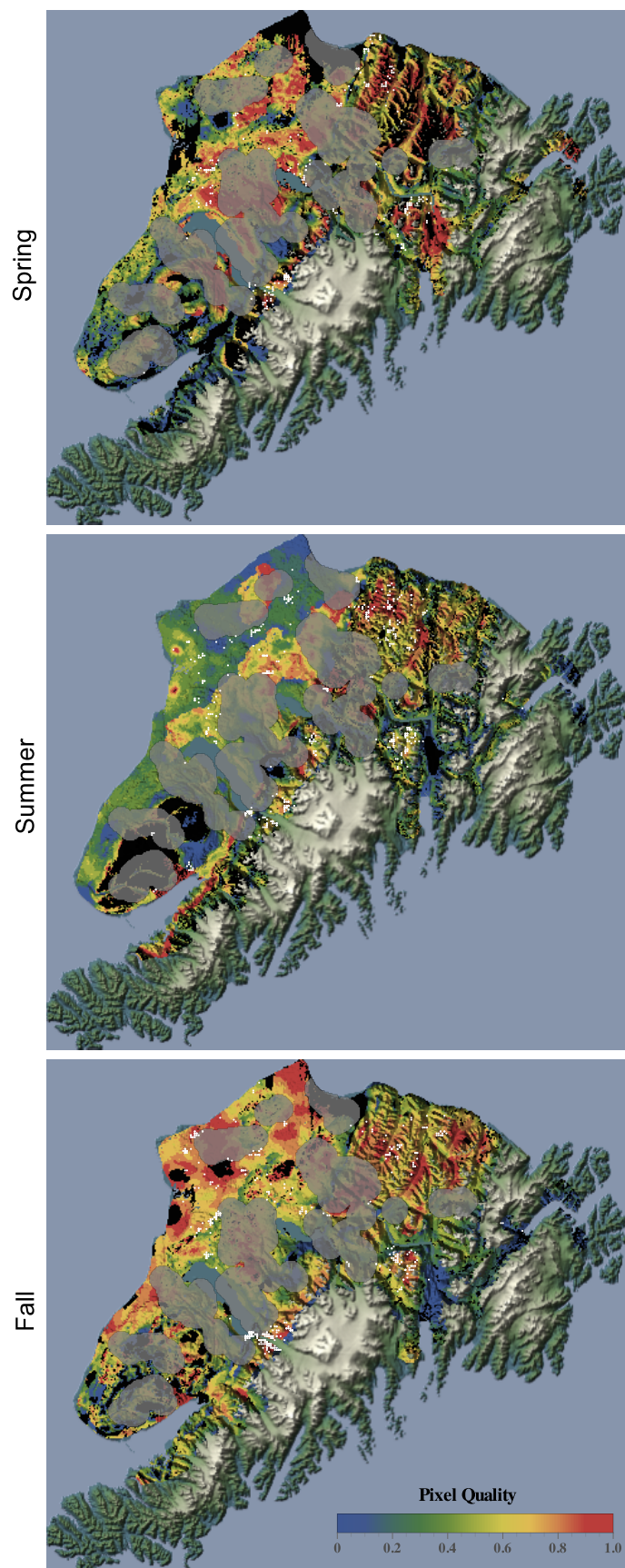
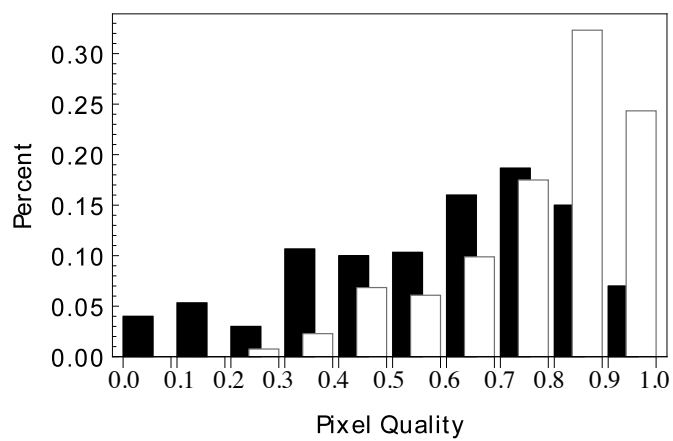
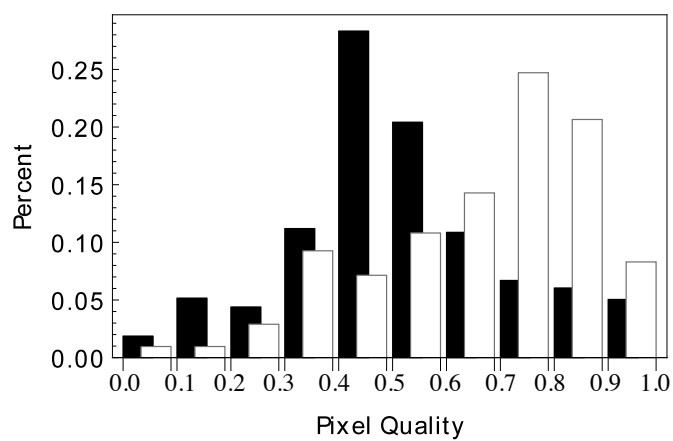


Figure 3.5. Absolute quality habitat preference maps in all four regions for each season. The maps were created using the parameter estimates from the best model. Pixels are scaled from blue (low quality) to red (high quality). Pixels within a 10-pixel radius of frequently visited streams are shaded gray, and pixels with landscape values outside of the acceptable extrapolation range are shaded black. Movement endpoints that were used to fit the models are shown in white.

Spring



Summer



Fall

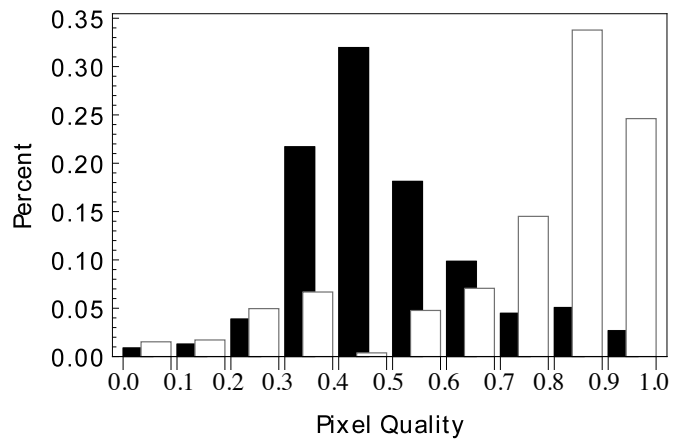


Figure 3.6. Histograms of the relative quality of the pixels chosen by bears during each season. Black bars represent pixels chosen within a 10-pixel radius of streams, and white bars represent pixels chosen outside of this radius.



Figure 4.1. Outline of the state of California, indicating the location and topography of the study site within Joshua Tree National Park (JOTR).

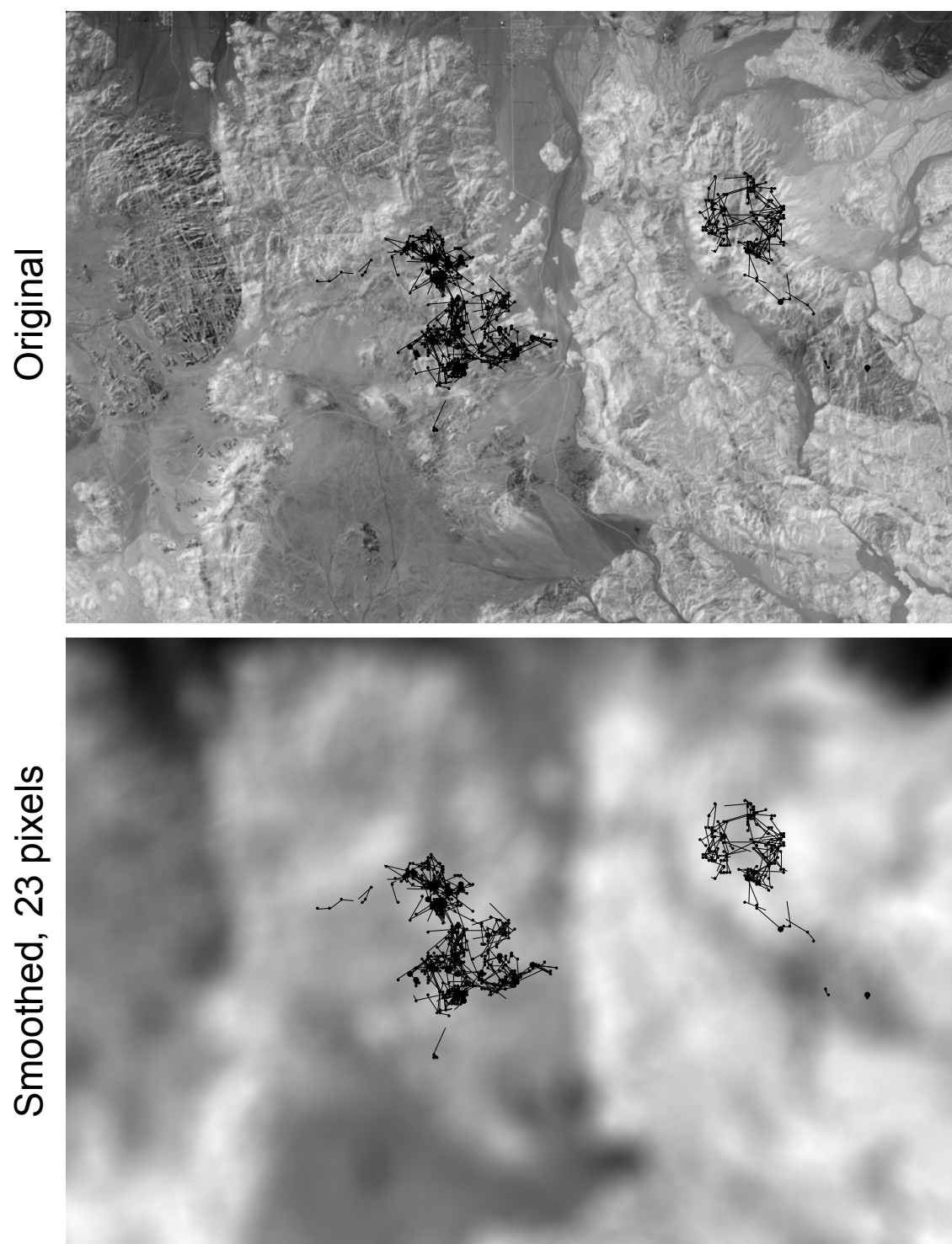


Figure 4.2. Vegetation layer, original (top) and smoothed with a 23-pixel radius kernel (bottom). Both maps were overlaid with transient sheep movement segments during the

spring; black points represent the end-point of each movement. This variable is higher in the eastern mountain range.

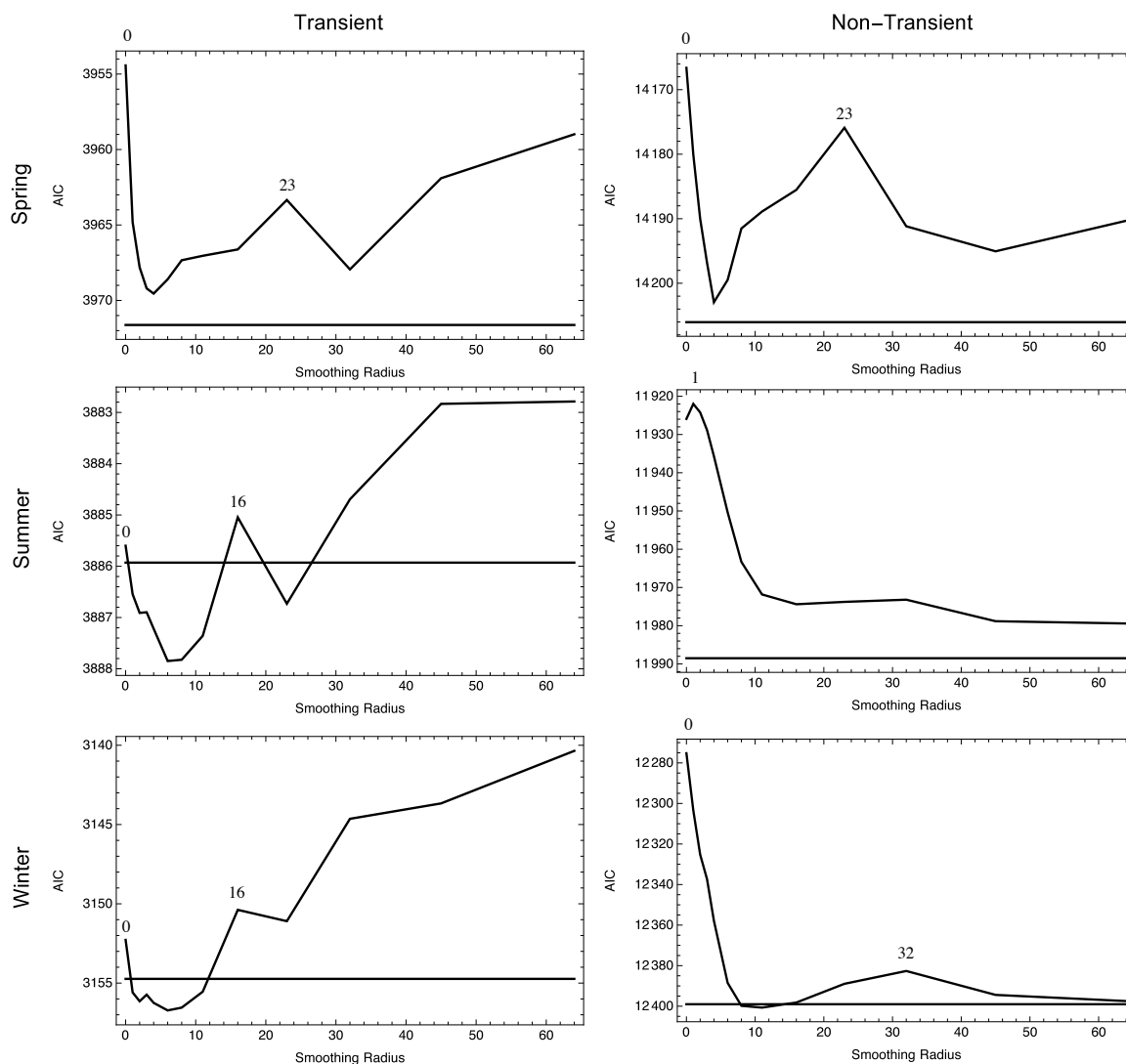






































Figure 4.3. Selection of the vegetation variable at multiple spatial scales for transient and non-transient sheep in each season. At each scale, the movement data is fit to four models: distance from the current location only, distance and the vegetation variable, distance and the vegetation variable squared, and distance with the linear and squared versions of the vegetation variable. Of the models that included the vegetation variable, only the one with the lowest AIC score is shown, along with the distance-only model (straight line), which was constant across all scales. Each of the peaks of model fit is

indicated. In all but one case (non-transient sheep during the winter smoothed at 32 pixels), the optimal scale included the squared version of the variable.

	Elevation	Slope	Ruggedness	Water Distance*	Vegetation (local)	Vegetation (regional)
Spring, Transient Main			3 		—	23 
Spring, Transient East			3 	—	—	23 
Spring, Non-Transient			1 	—	—	23 
Summer, Transient Main		—	3 		0 	—
Summer, Transient East**	—	—	—	—	—	—
Summer, Non-Transient			3 		1 	—
Winter, Transient Main			1 		—	16 
Winter, Transient East			1 	—	—	16 
Winter, Non-Transient			6 	—	0 	32 

*No permanent water present in east range.

**Too few data points to accurately determine sheep preferences.

Figure 4.4. Predictor variables and their functional shapes for each dataset. The shape of the relationship is only shown for variables that were present in the best model. The optimal scale (radius of smoothing kernel) is indicated for ruggedness and vegetation. Distance from current location was present and negative in all datasets (not shown).

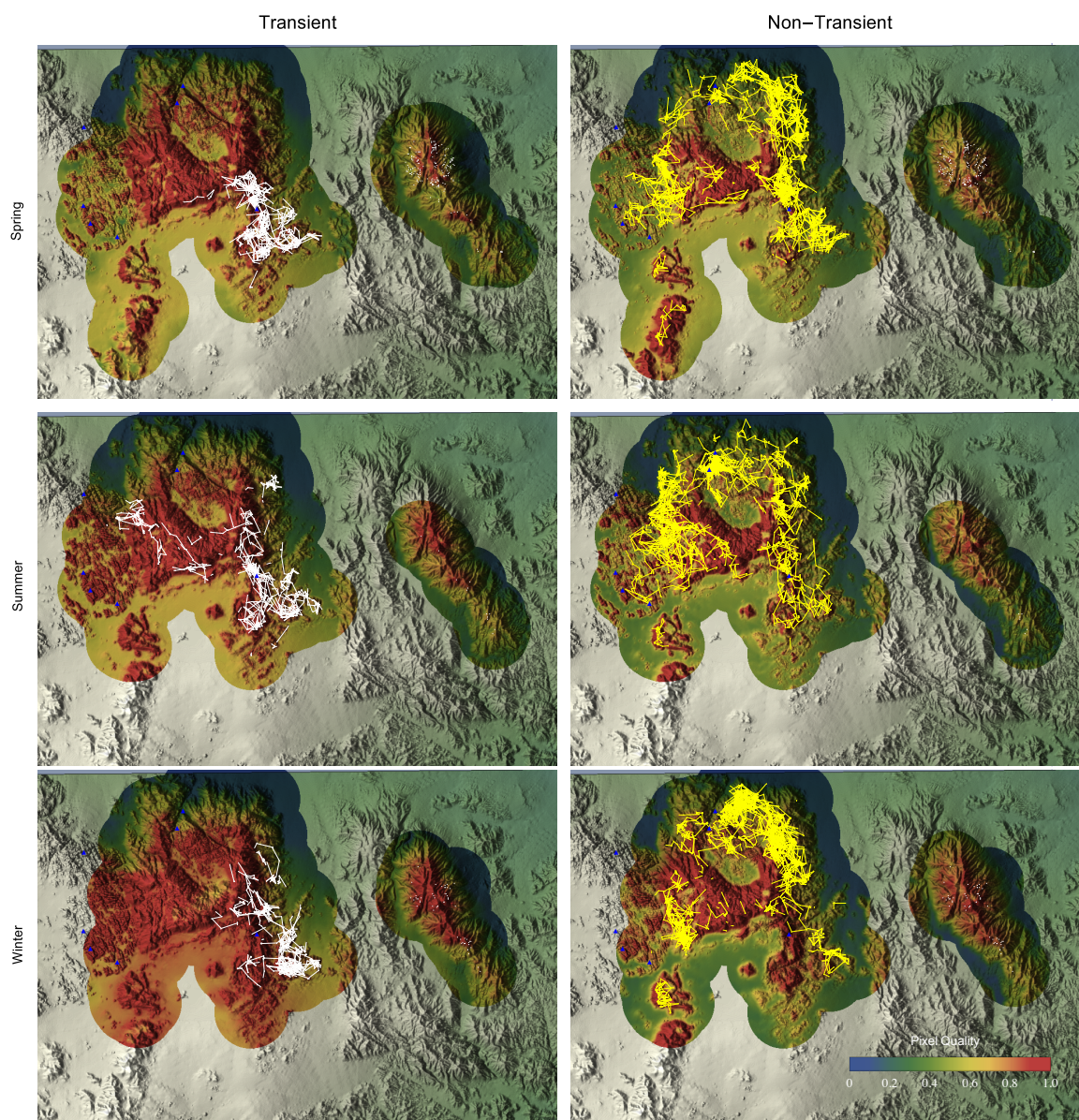


Figure 4.5. Habitat preference maps created using the parameter estimates for transient sheep (white) and non-transient sheep (yellow) movements in the main mountain range in each season. These parameter estimates were applied to the main range, which were overlaid with movement segments to demonstrate the quality of the pixels that were selected. The parameter estimates were then projected to the east range, which was overlaid with movement end-points of transient sheep to assess how well movements in

the main range predict high-quality habitat in the east range. Blue triangles indicate locations of permanent water.

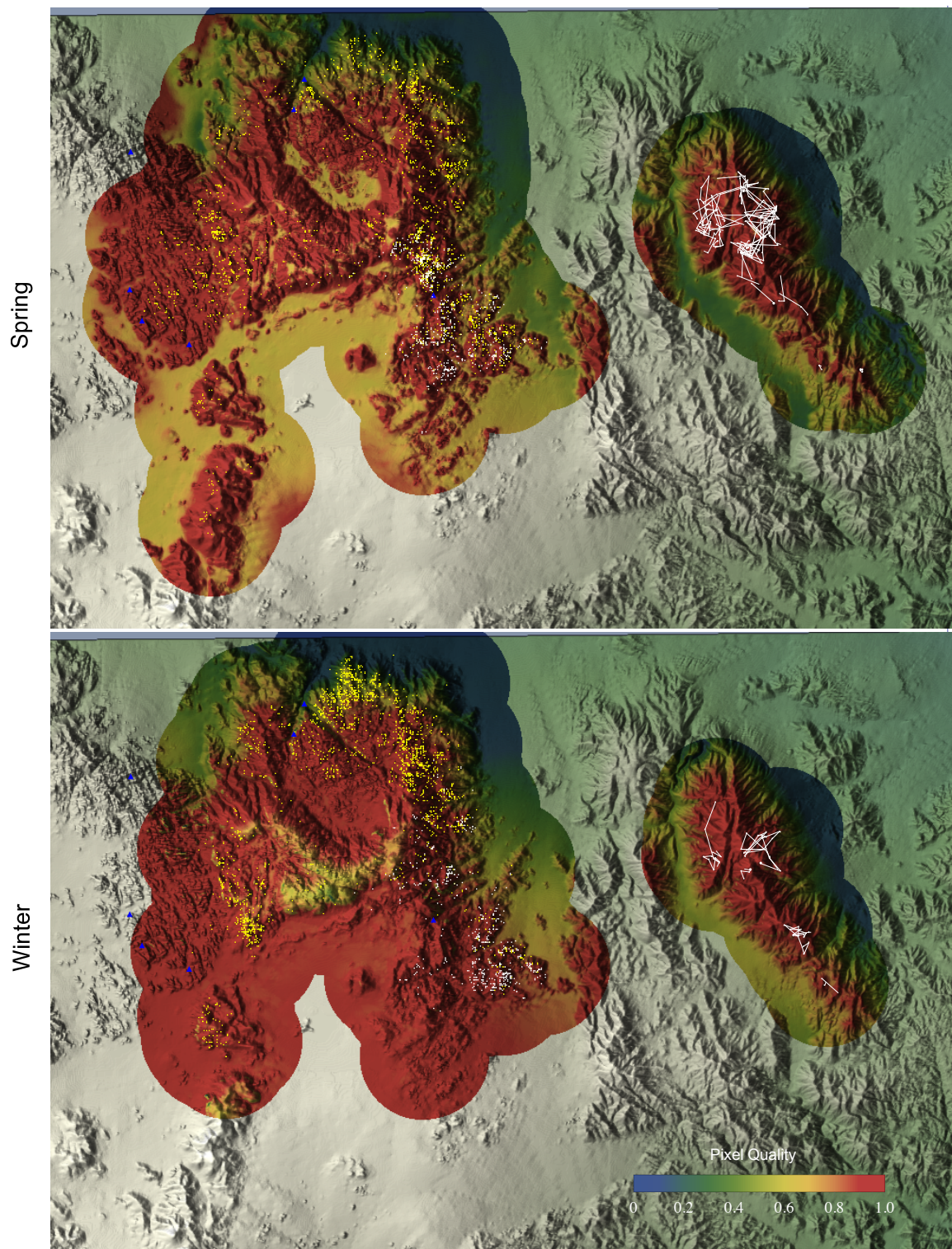


Figure 4.6. Habitat preference maps created using the parameter estimates for transient sheep (white) movements in the east mountain range in the spring and the winter (there

were not enough movements during the summer to project accurate preferences). These parameter estimates were applied to the east range, which was overlaid with movement segments to demonstrate the quality of the pixels that were selected. The parameter estimates were then projected to the main range, which was overlaid with transient (white) and non-transient (yellow) movement end-points to assess how well movements in the east range predict high-quality habitat in the main range. Blue triangles indicate locations of permanent water.