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Space Use and Reproductive Success of Male Sea Otters

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SPACE USE AND REPRODUCTIVE SUCCESS OF MALE SEA OTTERS

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by

Lily Maxine Tarjan

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Abstract

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By

Lily Maxine Tarjan

Animal space use determines access to resources, such as food and mates, and has implications for animal mating systems. Polygynous mating systems emerge when males, who typically exhibit low parental investment, monopolize females, who typically exhibit high parental investment, by defending patches of resources or aggregations of females. Defense of resource-containing territories incurs energetic costs and detracts time from essential activities such as foraging. Understanding mating systems is therefore key to interpreting processes that limit population growth in threatened species such as sea otters. Reproductive success of male sea otters may be related to defense of small territories (2–6 km^2) in shallow coastal waters. The absence of strong seasonal synchrony in female estrus requires that males defend territories year-round, suggesting a high cost to territory defense. My objectives were to: (1) characterize male space use, (2) quantify male reproductive success, and (3) describe the sea otter mating system. This research provided a new method of estimating animal space use in restricted habitats. The method estimates the probability of space use based on features of the physical environment (e.g. water depth) and effectively excludes unsuitable areas from home range estimates. I applied this method to VHF radio-telemetry data of 72 male sea otters in California and distinguished between three distinct space-use tactics, constituting territorial, satellite, and transient tactics. Tissue samples were collected from 67 males and 215 females in Monterey, California in 1999–2012. I assigned 37 microsatellite nuclear DNA markers to these samples, conducted paternity analyses, and provided the first estimate of male reproductive success in sea otters. Paternity analyses matched 40 father-pup pairs. Paternity assignments were low overall; individual males were assigned a maximum of 3 pups. Reproductive success peaked at seven years of age, and continued to 14. Territorial males who defended abundant kelp canopy experienced elevated siring success, but satellite males also sired pups. The sea otter mating system is thus characterized by resource defense polygyny. This work provides a foundation for synthesizing the energetic and reproductive tradeoffs of space-use tactics and better understanding the population biology of sea otters.

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Chapter 1

Introduction

Mating systems are an emergent result of individuals competing to maximize their lifetime reproductive success (Bradbury and Vehrencamp 1977, Clutton-Brock and Harvey 1978, Rubenstein and Wrangham 1986, Dunbar 1988, Reynolds 1996). Mammalian females often maximize reproductive success by investing resources in parental care, whereas males maximize reproductive success by competing for access to females (Trivers 1972, Kiyota et al. 2008). The degree to which males are successful at monopolizing population-wide reproductive output is characterized by the degree of polygyny (Kiyota et al. 2008) and the resulting variance in reproductive success across males is termed reproductive skew (Vehrencamp 1983, Keller and Reeve 1994, Reeve and Keller 1995).

In their seminal paper on mating system theory, Emlen and Oring (1977) described how monopolization of females is accomplished by either defending patches of resources or guarding females directly. As resources or females must be energetically defensible by an individual male, the environmental potential for polygyny relies on resource distributions. Scarce and evenly distributed resources afford little opportunity for mate monopolization. Abundant and patchily distributed resources, however, provide the potential for monopolization of multiple females by males. The evolution of polygynous mating systems also depends on the ability of males to capitalize on the potential for polygyny, which is often dictated by the amount of energy allocated towards parental care by males (Emlen and Oring 1977, Clutton-Brock 1989).

Male parental care is relatively rare among mammals (Trivers 1972), and more than 90% of mammalian species are described as habitually polygynous (Kleiman 1977, Rutberg 1983). Polygynous mating systems may be described along a continuum, defined at the extremes by resource defense polygyny and either female defense (Vanpé et al. 2009) or lekking polygyny, where males defend no resources (Alonso et al. 2012). The use of these strategies depends on the defensibility of females, which is directly influenced by female density, distribution, range size, group size and stability, and indirectly influenced by resource distribution (Clutton-Brock 1989). As females and resources exhibit different spatial and movement patterns, male space-use can indicate the means of mate acquisition within a population. In particular, male territoriality—or the act of defending an area against conspecifics (Begon et al. 2006)—is often associated with resource defense polygyny (Emlen and Oring 1977). Alternatively, males that utilize mate guarding as a means of increasing individual reproductive success are expected to follow female groups, forming a harem.

In resource defense polygyny, males anticipate how resources will affect female distribution and defend resource-rich areas to increase their access to mates (Emlen and Oring 1977). For territory defense to be economically feasible, the benefits must outweigh the energetic costs to the individual (Brown 1964, Davies 1978, Macdonald 1983, Powell 2000, Begon et al. 2006). The suggested benefits of territoriality are access to mates and exclusive or preferential use of resources (Powell 1994). Studies illustrating the use of resource defense polygyny have identified food (African impala and waterbuck) (Jarman 1974), the density of protective vegetation (red-winged blackbird) (Lenington 1980), and roosting sites (*Pipistrellus nanus*) (O'Shea 1980) as resources that males defend to maximize individual reproductive success.

Where female or resource defense is not energetically feasible, strong polygyny may still result if female choice acts to bolster differential reproductive success across males (Harcourt et al. 2007). Males may congregate near hotspots, or areas of high female density or female movement (Bradbury and Gibson 1983), thus increasing their encounter rates with receptive females and facilitating female choice between males (Bradbury 1981). In the presence of female choice, male attributes may influence the reproductive success of individual males. Female mate choice may be based on male characteristics that increase female fitness, such as genetic quality (Searcy 1979, Yasukawa 1981), or on features to which females have a preexisting sensory bias (West-Eberhard 1984). Females may infer the genetic quality of males using cues such as age (Weatherhead and Robertson 1981, Weatherhead 1984, Weatherhead and Boag 1995, Wetton et al. 1995). In many systems, female mate choice is based on a complex interaction of genetic attributes that enhance male quality and diverse resource attributes that affect territory quality (Yasukawa 1981, Sikkel 1995).

Studies of pinnipeds, which have greatly advanced theories of the evolution of mating systems, have often neglected the role of female choice in mating behavior (Gemmell et al. 2001). The degree of polygyny in pinniped mating systems is largely determined by environmental characteristics of the breeding site (Stirling 1983, Le Boeuf 1991). High levels of polygyny result when females are concentrated in limited, terrestrial haul-outs required for parturition, such as in elephant seals that exhibit extreme harem defense polygyny (Bartholomew 1970). Low levels of polygyny occur when species, such as harbor seals, mate aquatically, rendering it difficult for males to monopolize mates that are highly mobile in the marine environment (Coltman et al. 1998, Fabiani et al. 2004, Harcourt et al. 2007). Although it is often assumed that female seals mate with the male occupying the territory in which she enters estrus (Gemmell et al. 2001), mate choice studies suggest that female preference may play a significant role in some pinniped mating systems (e.g. fur seals) (Goldsworthy et al. 1999). In particular, female choice may be an important determinant of male reproductive success in aquatically mating pinnipeds, where females have a greater opportunity to manage intersexual encounters (Gemmell et al. 2001).

Southern sea otters (*Enhydra lutris nereis*) present an opportunity to broaden and further develop theories of mammalian mating systems in the ocean. Despite a recent invasion of the marine environment—sea otters are one of the most recently evolved marine mammals—sea otters have severed all ties to a terrestrial existence, and mating is exclusively aquatic. In contrast to terrestrial carnivores of similar size, sea otters are found at high densities, perhaps as a consequence of abundant invertebrate prey. The sea otter mating system differs from those of seals and sea lions because females are asynchronous breeders and parturition/pup rearing is aquatic, precluding the potential to monopolize female breeding aggregations. Some males defend aquatic territories, while females have annual home ranges that encompass multiple male territories.

Territorial males must defend territories year-round to capitalize on females that forage, rest, groom, and socialize within these areas and that may come into estrus at any time. Mating system theory predicts that both absolute synchrony and total asynchrony of sexual receptivity decrease the potential for males to monopolize females (Emlen and Oring 1977). Synchronous estrus and spatial aggregation in pinnipeds is facilitated to some degree by the ability of females to rely on fat reserves and geographically disassociate foraging and breeding. In contrast, asynchronous estrus means that estrous females are dispersed across time, so it is difficult for males to monopolize groups of females. In comparison to pinnipeds, sea otters exhibit low ssynchrony in breeding. Pups are born in every month and sea otters breed throughout the year (Barabash-Nikiforov 1935, Fisher 1940, Murie 1940, Kenyon 1959, Lensink 1962, Sinha et al. 1966, Riedman et al. 1994), with some evidence for peaks in breeding activity (Lensink 1962, Sinha et al. 1966, Riedman et al. 1994). Low synchrony may be related to energetic requirements. Sea otters are extreme income strategists so are unable to dedicate time exclusively to reproduction; their feeding, resting, and mating activities overlap in time and space.

The territory resources and/or male attributes that influence male reproductive success are unknown in this species. Furthermore, the reproductive role of non-territorial males, which rest outside of territorial areas but may nonetheless copulate with females, has never been described. The overall objectives of my project are threefold: (1) to determine reproductive success and reproductive skew in male sea otters, (2) to identify individual and territory features that confer high male reproductive success, and (3) to quantitatively describe the sea otter mating system and identify its primary drivers.

To accomplish these objectives, I measured the effects of individual attributes, patterns of space use, and territory resources on the reproductive success of radio-tagged males in Monterey Peninsula, CA. My second chapter addresses the prerequisite of estimating male home ranges in sea otters. As available methods of home range estimation perform poorly in this species, designing a method to delineate home range and territory boundaries was necessary to evaluate territory quality. The third chapter focuses on quantifying reproductive success and reproductive skew in male sea otters using microsatellite paternity analysis. In the fourth chapter, I quantify male attributes and territory features and analyze their effect on individual reproductive success.

Chapter 2

Permissible Home Range Estimation (PHRE) in restricted habitats: a new algorithm and an evaluation for sea otters

Abstract

Parametric and nonparametric kernel methods dominate studies of animal home ranges and space use. Most existing methods are unable to incorporate information about the underlying physical environment, leading to poor performance in excluding areas that are not used. Using radio-telemetry data from sea otters, we developed and evaluated a new algorithm for estimating home ranges (hereafter Permissible Home Range Estimation, or “PHRE”) that reflects habitat suitability. We began by transforming sighting locations into relevant landscape features (for sea otters, coastal position and distance from shore). Then, we generated a bivariate kernel probability density function in landscape space and back-transformed this to geographic space in order to define a permissible home range. Compared to two commonly used home range estimation methods, kernel densities and local convex hulls, PHRE better excluded unused areas and required a smaller sample size. Our PHRE method is applicable to species whose ranges are restricted by complex physical boundaries or environmental gradients and will improve understanding of habitat-use requirements and ultimately, aid in conservation efforts.

Introduction

Home range estimates are useful tools for answering critical questions in studies of habitat selection (Cavallini and Lovari 1994, Dickson and Beier 2002, Thomas and Taylor 2006), mating systems (Hedmark et al. 2007, Vanpé et al. 2009), and carrying capacity (Mitchell and Powell 2012), and in identifying the biotic and abiotic features with which individuals interact. Statistical methods for estimating home ranges, defined as the particular area to which an animal restricts its movements over time (Seton 1909, Burt 1943), use sighting locations to estimate the probability of an individual occurring at any point in space, and to delineate a boundary encompassing some cumulative probability of occurrence. These boundaries denote the location, shape, and size of the home range (Moorcroft 2012).

A notable limitation of existing methods is their inconsistent performance across species and habitats (Fieberg and Börger 2012, Powell and Mitchell 2012). Current methods typically perform well for animals that make indiscriminant use of open, uniform habitats, but poorly for animals that concentrate space use around patchy resources (e.g., tawny owls [*Strix aluco*] in woodland patches [Redpath 1995] and red-capped robins [*Petroica goodenovii*] in woodland remnants [Major and Gowing 2001]) or are restricted by complex boundaries (Mitchell and Powell 2012) (e.g., river otters [*Lontra candensis*] at the aquatic-terrestrial interface [Blundell et al. 2001], flathead catfish [*Pylodictis olivaris*] in streams [Vokoun 2003], weasels [*Mustela nivalis*] inhabiting field edges [MacDonald et al. 2004], and raccoons [*Procyon lotor*] along habitat edges [Barding and Nelson 2008]). In the latter case, existing methods generally fail to exclude unusable habitat (White and Garrott 1990, Getz and Wilmers 2004, Getz et al. 2007, Knight et al. 2009). This positive bias (type II error) causes an overestimate of home range area and affects our ability to understand patterns of resource use and exposure to sources of mortality.

Current methods derive home range estimates from sighting locations anchored in “geographic space,” generally defined using a two-dimensional Cartesian coordinate system such as latitude and longitude. However, animal space use is often determined by ecological characteristics, which are defined by environmental features and/or the space use of conspecifics and other species. Hence, there is often a mismatch between how we estimate home ranges and how animals actually choose their home ranges, so we should not be surprised that our methods sometimes perform poorly. A number of modifications to traditional home range analyses have been proposed to address this issue; for example, Horne et al. (2008) created a synoptic model of animal space use that produces home ranges informed by habitat covariates. Although this method can be applied to animals whose home ranges track a linear habitat feature (Slaght et al. 2013), the accuracy of the so-called “null distribution” of the synoptic model decreases as the linear feature becomes more tortuous. Take, for example, the case of a strictly marine species that uses one side of a peninsula. Although the presence of water (1) or land (0) can be added as a binomial habitat covariate, the null distribution will cause points on one side of the peninsula to influence probability values on the other side of the peninsula, even if the animal is only found on a single side. This is because the two sides of the peninsula are close to each other in geographic coordinate space, but are far apart from the perspective of an animal traveling through the water. Home range analysis in such cases remains problematic; in particular, it remains difficult to derive home range estimates that do not violate known habitat restrictions for species with tortuous linear boundaries in their habitat.

Mechanistic movement models offer a sophisticated method for incorporating environmental covariates (e.g. coyote prey and conspecific scent marks) (Moorcroft et al. 1999) into animal movement decisions. Home range estimates can be derived from such movement models, as employed in Mechanistic Home-Range Analysis (MHRA) (Moorcroft et al. 1999). This powerful approach confers the ability to predict future movements, but may be unnecessarily complex for obtaining descriptions of past home ranges. As pointed out in Moorcroft's review (Moorcroft 2012), MHRA is challenging to implement as it requires programming expertise, is computationally expensive, and/or requires familiarity with formulating and solving systems of differential equations. These challenges may explain the persistent and widespread use of simpler descriptive methods of home range estimation. We aimed to provide an accessible method with the explicit purpose of describing the observed space use of an animal.

As with many coastal species, sea otter (*Enhydra lutris*, Linnaeus 1758) space use is restricted by the complex coastal boundary and the heterogeneous habitats that characterize nearshore environments. Sea otters live predominantly in aquatic areas, and avoid hauling out more than a few meters inland due to poor motility on land, vulnerability to terrestrial predators, and their requirement for frequent feeding bouts in the ocean. In addition, physiological limits in diving capabilities restrict sea otters to areas where benthic invertebrate prey are accessible (generally <40 meters depth) (Bodkin et al. 2004, Thometz et al. 2014). Despite the >76,000 radio-telemetry sighting locations of individual sea otters collected to date from studies in central California (Tinker et al. *in review*) and the wealth of knowledge about sea otter habitat requirements, a suitable home range estimator is lacking. Home ranges created using kernel density estimation (KDE) (Silverman 1986, Worton 1989) and adaptive Local Convex Hull analysis (a-LoCoH) (Getz and Wilmers 2004) typically overlap with terrestrial areas that are too far inland to be accessible to sea otters and/or include aquatic areas that are too far offshore or too deep, leading to incorrect expectations about access to resources and home range size and shape. To address this problem in sea otters and other species with similar restrictions to movement, we present a novel analysis that incorporates features of habitat suitability (boundaries and environmental gradients) into home range estimates (i.e. geographic ranges of animals in space).

Using radio-telemetry data on sea otters, we develop and evaluate a method for estimating permissible home ranges (hereafter "Permissible Home Range Estimation," or PHRE) that: (1) reflects ecological and physiological constraints on animal movements, (2) generates probability estimates based on habitat suitability, and (3) produces robust, unbiased estimates of the areas actually used by individual sea otters. We describe a generalized function for PHRE coded in the open source statistical program R (R Development Core Team 2013). In addition, we evaluate and compare sample size requirements and the predictive accuracy of probability estimates of PHRE and two commonly used methods: kernel density estimation and Local Convex Hull Analysis. We then use this new method to test the prediction that resource distribution across sites in central California affects the shape of sea otter home ranges.

Methods

Ethics statement

This research adhered strictly to established capture, tagging, and tracking protocols, which were reviewed and approved by the University of California Santa Cruz Institutional Animal Care and Use Committee and the U.S. Fish and Wildlife Service. Protocols were conducted under the following research permits: University of California Santa Cruz IACUC permit Tinkt1007 (8/05/2010) and U.S. Fish and Wildlife Service permit MA672624-16 (10/31/2008). As outlined and approved in the established protocols, animals were sedated for surgery with an intramuscular injection of fentanyl (Elkins-Sinn, Cherry Hill, NJ, USA; 0.5–0.11 mg kg^{-1} body mass) and diazepam (Abbot Laboratories, North Chicago, USA; 0.010–0.053 mg kg^{-1}) and maintained under an isoflourane gas and oxygen mixture (Williams and Siniff 1983).

Data collection

From 1999 to the present, U.S. Geological Survey and Monterey Bay Aquarium scientists and volunteers collected spatially explicit sighting data from radio-tagged sea otters near Monterey Bay (36.6183° N, 121.9015° W) and Big Sur, California (36.1075° N, 121.6258° W). We captured sea otters using rebreather SCUBA and Wilson traps (Ames et al. 1986), surgically implanted them with VHF radio transmitters (Advanced Telemetry Systems Inc., Isanti, MN, USA), and applied color-coded plastic flipper tags in the webbing of the hind flippers (Temple Tags, Temple, TX, USA) to aid in visual identification (Williams and Siniff 1983, Monson et al. 2001).

We visually located tagged individuals during regular field surveys (usually 3–5 times per week, but less often for some wide-ranging individuals) using standard VHF radio telemetric techniques (Ralls et al. 1996, Tinker et al. 2006a) for multiple years. This resulted in 38,941 sighting locations for 193 individuals. While autocorrelation is of concern in home range estimation, sea otters routinely travel the full length of their home range in a single day, so we treated the sighting locations (which are only collected every few days) as independent. Associated observational data collected at the time of each sighting confirmed that all sighting locations were in water, and that terrestrial areas represented unused habitat. Sighting locations from 126 sea otters with >20 sighting locations per individual over a two-year period were used to compare the performance of three home range estimation methods. Because home range boundaries often change over an animal's lifetime (e.g. male sea otters disperse as juveniles and may settle into small reproductive territories as adults) (Ralls et al. 1996) and comparisons are meaningful only if home ranges are calculated over the same time period (Fieberg and Börger 2012), we used two years of data for each home range estimate.

Model Description

PHRE consists of four steps: (1) identify habitat elements that influence animal space use a priori, (2) transform sighting locations to a new coordinate system reflecting key habitat variables, (3) produce a kernel density estimate in landscape space, and (4) back-transform the KD probability values to geographic coordinate space. For sea otters that move primarily up and down the coast within the nearshore environment, the key habitat elements defining space use are position along the California coastline and distance from shore (Figure A1). Coastal position in California is easily described by a previously-defined one-dimensional axis termed the "As The Otter Swims" (ATOS) line, representing a sequentially numbered set of points at 500-m intervals along the 10-m isobath (Pattison et al. 1997) (Figure A2). Each sighting location was transformed to decimal ATOS units by linear interpolation (e.g. a sighting location that was 1/3 of the way between ATOS point 367 and 368 was assigned a value of 367.33). The perpendicular distance to the closest shoreline feature was also calculated for each sighting location using the 1:24,000 coastline vector (California Department of Forestry and Fire Protection 2007). The resulting transformed coordinate system better reflected movement decisions by the animal (i.e. animals decide to move up or down the coast, and on or off shore), and also flattened out the tortuous linear boundary.

We further transformed the distance-from-shore values to ensure complete exclusion of terrestrial areas from home range estimates and to normalize the right-skewed distribution. Specifically, we log-transformed the raw distance-from-shore values (Figure A3), which resulted in a distribution that was approximately normal, varied in log-space from $-\infty$ to ∞ and, importantly, prohibited assignment of probability values >0 on land because log(0) is undefined. We note that for boundaries having an environmental value other than 0, or for environmental variables where log-transformation is not appropriate, an alternative approach is to use a truncated normal distribution for the kernel along the target axis. These practices are key to complete exclusion of unused areas when a distinct boundary exists, especially if the animal heavily uses areas immediately adjacent to the boundary.

We next fit a bivariate kernel density function (ks package [Duong 2014] in R version 3.0.2 [R Development Core Team 2013]) using the decimal ATOS and *log*(distance) variables for each individual (Figure A4). Otters are known to differ in the nature of their coastal movements, with some individuals (e.g. adult females) making small movements and using a highly concentrated area of coast, and other individuals (e.g. juvenile males) making longer movements and utilizing large areas of the coast (Tinker et al. 2008b). To account for these different space-use patterns we used an adaptive smoothing parameter (h) for the decimal ATOS axis. We allowed the value of h to vary as a function of the mean nearest neighbor distance (d) between sighting locations, according to the equation $h = h_b \cdot (d/4)^{2.5}$, where h_b represents the baseline smoothing parameter of 2 ATOS units, or 1 km of coastline. This equation was selected prior to home range analyses using a subset of animal location data and based on subjective visual choice (Silverman 1986, Wand and Jones 1995, Calenge 2011) of a parameter that consistently avoided under- and over-smoothing for a variety of different movement types (i.e. those represented by adult females, juvenile males, and adult males). The smoothing parameter for the *log*(distance) axis was held fixed at 0.05.

The kernel density function was then back-transformed to geographic space by evaluating the probability density values across a grid of points with local coverage (Figure A5). All density values in the grid were then transformed to sum to one and reflect probability values. A polygon was created to encompass grid points within the 90% kernel home range boundaries (Figure 2.1 & Figure A6). We created a function that applies the above-described algorithm to any dataset, using the open source statistical programming language R (version 3.0.2) (R Development Core Team 2013) and incorporating the ks (Duong 2014), raster (Hijmans 2014), and amap (Lucas 2014) packages. This generalized function requires sighting locations and a list of raster datasets with habitat elements of interest (the analysis handles one to six dimensions in landscape space). Optional specifications include the percent kernel and the smoothing parameter.

Method Comparison

We evaluated the method's utility by comparing its general performance with two other commonly used methods of estimating home ranges in geographic space: (1) kernel density estimation (KDE) (Silverman 1986, Worton 1989) and (2) adaptive Local Convex Hull analysis (a-LoCoH) (Getz and Wilmers 2004), a nonparametric method designed to delineate habitat boundaries. We used the ks package (Duong 2014) for KDE and the adehabitatHR package (Calenge 2006) for LoCoH. The baseline smoothing parameter was 30,000 for KDE, which we then adapted for each animal using the same method as applied in PHRE. As suggested by Getz et al. (2007), we used the maximum distance between sighting locations of the animal being evaluated for the LoCoH smoothing parameter. All three methods therefore adapted the smoothing parameter according to the distribution of sighting locations for each animal. We selected 90% isopleths as home range boundaries (Figure 2.1). The performance of each method was then evaluated based on the following metrics: (a) the ability to exclude unused (terrestrial) areas from home range estimates, (b) the minimum sample size of sighting locations required, and (c) the predictive accuracy of probability estimates.

Exclusion of unused areas

To test the ability of each method to exclude terrestrial areas, we calculated the percent of home range area that overlapped with terrestrial habitat (1:24,000 shoreline feature) using the rgeos package (Bivand and Rundel 2015) in R version 3.0.2 (R Development Core Team 2013).

Sample size requirement

We iterated home range estimates across different sample sizes of sighting locations ($N = 10$ to 300 in increments of 10) using data for 26 animals with ≥300 sighting locations within a two-year period. For each sample size, we subsampled data without replacement ten times. We identified the minimum sample size requirement (defined as the minimum N that produced mean home range areas statistically similar to the estimated area at $N = 300$) (Bekoff and Mech 1984) for each animal using a Kruskal-Wallis test and Wilcoxon rank sum tests with a Bonferroni correction (adjusted cutoff value at $p = 0.0167$) across sample sizes (data were non-normally distributed, Kolmogorov-Smirnov test, $p << 0.05$) and compared requirements across methods. To address variation around mean area, we fit an asymptotic curve to the coefficient of variation (CV) and determined at what N the CV reached an asymptote. We compared CV sample size requirements across methods using a one-way analysis of variance (ANOVA) executed with the aov function (data were normally distributed within methods, Kolmogorov-Smirnov test, $p >> 0.05$).

Predictive accuracy of probability estimates

For 26 animals with ≥300 sighting locations, we generated home range estimates for each method using 200 sighting locations (greater than the maximum sample size requirement for all methods; see results below). Rather than restrict estimates to simplified 90% isopleth boundaries, we tested the predictive accuracy of the probability grids from PHRE and KDE and created probability grids for LoCoH using the 10–100% isopleths (at 10% intervals). We evaluated all methods on their ability to predict the location of 100 randomly selected sighting locations (presence points)—independent from those used for the home range estimate—against a background sample of 1,000 pseudo-absence points, which were randomly drawn from within 1 km of the sighting locations. We iterated this process ten times and calculated the average area under the receiver operating characteristic curve (AUC) (Metz 1978, Hanley and McNeil 1982, Fielding and Bell 1997) for each method using the dismo package (Hijmans et al. 2011) in R. AUC is a threshold-independent measure of model performance that calculates the proportion of pixels correctly or incorrectly classified. The receiver operating characteristic curve depicts the relationship between the proportion of correctly predicted presences (i.e. the true positive rate) against the proportion of incorrectly predicted absences (i.e. the false positive rate). AUC ranges from 0.5 for a model that is no better than chance to 1.0 for a model that perfectly predicts presences and absences. AUC values did not meet assumptions of a normal distribution (Kolmogorov-Smirnov test, $p < 0.05$), so we compared across methods using a Kruskal-Wallis test and Wilcoxon rank sum tests with a Bonferroni correction (adjusted cutoff value at $p = 0.0167$).

An Ecological Application

In addition to comparing the methods, we used all three home range estimators to test predictions about the effects of habitat structure on sea otter space use. Home ranges should result from animals maximizing benefits—resources contained within an area—while minimizing costs of travel and resource extraction (Mitchell and Powell 2012), so size and shape should be influenced by resource availability and distribution. Due to physiological limits in sea otter diving capabilities (Bodkin et al. 2004, Thometz et al. 2014), the continental-shelf extent has a large impact on offshore availability of benthic prey. Among study sites for this project, Monterey Bay has a more extensive continental shelf than Big Sur, so sea otters are capable of accessing prey resources farther offshore in Monterey Bay. We hypothesized that size and shape of home ranges are influenced by these differences in resource distribution between sites.

We quantified the amount of available habitat in Monterey Bay and Big Sur, CA based on coastal bathymetry. We used 200-m resolution bathymetry data (California Department of Fish and Game Bathymetry Project & State of California Teale Data Center GIS Solutions Group 2002) to select areas that are accessible to diving sea otters (0 to −39 m depth, which encompasses the 99th percentile of diving depths for sea otters in Monterey Bay and Big Sur [Tinker et al. *in review*]). We tested our hypothesis that habitat bathymetry affects home range shape by plotting home range length (the distance along the “as the otter swims” line [10-m isobath] encompassed within the home range polygon) vs. home range area—where slope represented the length-area relationship (i.e. home range shape)—and comparing the slopes between sites. Higher slopes in this case indicate more elongated home range polygons. We compared the ability of each method to detect differences in home range shape between sites by evaluating the assumption of homogeneous slopes of fitted, log-linearized functions using analysis of covariance (ANCOVA; data were normally distributed; Kolmogorov-Smirnov test, $p > 0.1$) (R Development Core Team 2013).

Results

Method Comparison

Exclusion of unused areas

KDE resulted in home range estimates that overlapped the most with terrestrial habitat (13.59 [10.15, 18.10]% of home range area was on land; note that statistics are presented as median [quartile 1, quartile 3]), and LoCoH overlap was intermediate (2.67 [0.43, 7.30]%; Wilcoxon rank sum test of LoCoH versus KDE, $W = 2321$, $p < 0.0001$). At the extreme, the maximum overlap was higher for LoCoH (53.64%) than for KDE (32.22%), but more LoCoH home ranges (18 out of 126) completely excluded land than KDE home ranges (0 out of 126). PHRE home ranges completely avoided overlap with land, as the method defines the probability of unused areas as zero (Figure 2.2). Note that the precision of PHRE home range boundaries depends on the resolution of the grid across which the probability values are estimated, so minimal overlap (<1%) can result if the resolution of the estimation grid is lower than the resolution of the unusable habitat spatial data.

Sample size requirement

By iterating home range estimates across sample sizes of sighting locations, we found that PHRE required the fewest sighting locations (N =10 [10, 20]; chi-squared = 9.92, df = 2, p = 0.007; W = 417, p = 0.006). KDE required 50 (10, 80) sighting locations, while LoCoH polygons required 40 (10, 80) sighting locations. The requirements set by the coefficients of variation were statistically similar across methods (df = 2, F = 0.87, p = 0.42) and suggested using 210 (190, 230) sighting locations to minimize variation in estimated areas (Figure 2.3). Note that average area differed by method (log-transformed data were normally distributed, Kolmogorov-Smirnov test, p = 0.72; one-way ANOVA and Tukey HSD, df = 2, F = 27.53, p <0.0001), with PHRE tending to produce the largest home ranges (4.10 [2.29, 7.14] km^2), KDE producing home ranges of intermediate area (3.23 [1.85, 5.04] km^2), and LoCoH producing the smallest (1.81 [0.70, 3.41] km^2). Area of the 90% polygon was sensitive to the smoothing parameter (which was not directly comparable across methods), so we withheld interpretation of polygon area and instead used a threshold independent analysis to address predictive accuracy of the probability estimates.

Predictive accuracy of probability estimates

All methods produced home range probability estimates that predicted locations of presence and pseudo-absence data better than chance (Figure 2.4). KDE and PHRE had high predictive accuracy (AUC = 0.98 ± 0.01 [mean ± standard deviation] and 0.97 ± 0.02 respectively), and LoCoH had lower predictive accuracy (AUC = 0.93 ± 0.02; $df = 2$, chi-squared = 454.26, $p < 0.0001$). Receiver operating characteristic curves showed that LoCoH displayed low true positive rates, indicating exclusion of used areas and negative bias (type I error). While KDE had the highest AUC values, the performances of KDE and PHRE were qualitatively similar, and both generally avoided negative (type I error) and positive bias (type II error).

An Ecological Application

Based on PHRE home range estimates, a typical 8.6-km stretch of coastline (the average home range length for otters in both habitats) contained 7.23 km^2 of accessible area for benthic foraging in Monterey Bay and 5.10 km^2 in Big Sur (Figure 2.5). To determine whether sea otter space use reflected these differences in available habitat, we compared home range shapes using the slopes of log-linearized functions representing the length-area relationship. The interaction term for the full linear model (Length ~ Area + Site + Area : Site) was statistically significant for KDE ($df = 122$, $t = -0.12$, $p = 0.03$), LoCoH ($df = 122$, $t = -0.13$, $p = 0.01$), and PHRE ($df = 122$,

$t = -0.24$, $p = 0.01$), indicating that the assumption of slope homogeneity was not supported (Figure 2.6). Based on the magnitude of the difference between slopes of the linear models (and therefore the difference in home range shapes between sites), PHRE showed the largest effect size, where home range length was greater in Big Sur than in Monterey Bay (difference in slope coefficients = 0.24 ± 0.11 for PHRE, and 0.12 ± 0.06 and 0.13 ± 0.06 for KDE and LoCoH respectively). To interpret the biological significance of this difference, we calculated the expected difference in home range length in Big Sur versus Monterey Bay. Our analysis using PHRE indicates that a home range of average area (5.30 ± 4.24 km^2) is 1.16 km longer in Big Sur compared to Monterey Bay. A home range of maximum area for Big Sur (14.07 km^2) is 8.47 km longer than the equivalent home range in Monterey Bay.

Discussion

Methods of describing animal space use have improved in their ability to incorporate complex environments. Non-parametric kernel estimation methods require fewer assumptions about patterns of animal space use than do parametric density functions or minimum convex polygons (Anderson 1982, Worton 1989). Local Convex Hull analysis (Getz and Wilmers 2004) allows for the identification of moderately complex boundaries, and the lattice-based density estimator (Barry and McIntyre 2011) allows for recognition of quite complex boundaries. However, while species distribution models use habitat variables to inform predicted distributions (see Guisan & Zimmermann [2000] for a review), home range estimates rarely incorporate continuous habitat features a priori (but see Horne et al.'s [2008] synoptic model of animal space use and Moorcroft et al.'s [1999] Mechanistic Home-Range Analysis for a sophisticated application of this concept using movement models). Habitat selection analyses (such as maximum entropy [Phillips et al. 2006] or general additive mixed models [Skern-Mauritzen et al. 2011]) make use of such non-Cartesian dimensions, but they serve a fundamentally different purpose from home range analysis. PHRE is one of the first methods to directly incorporate continuous features of the environment in probability estimates of past space use by an individual. PHRE performed well in including used areas and excluding unused areas, allowing for meaningful statistical descriptions of home range use in complex, restricted habitats.

Method Comparison

Exclusion of unused areas

PHRE proved to be more successful at excluding terrestrial areas than the other two home range methods. This is perhaps not surprising, given the methods of coordinate transformation (PHRE disallows any overlap with land, as unused areas receive a probability estimate of zero by definition). This particular feature of PHRE will be extremely useful for coastal-dwelling marine species such as sea otters, or other species where a complex "hard boundary" needs to be accommodated in home range methods. PHRE was more successful at this task than LoCoH, which also recognizes hard boundaries in animal space use (Getz and Wilmers 2004). However, PHRE requires that the feature(s) of unusable space be identified a priori, whereas LoCoH can highlight such boundaries with no a priori information. Thus if the goal is to estimate home ranges when there is suspicion of hard boundaries (but no means to pre-identify unusable space), then LoCoH would be a more suitable method, but if there are complex boundaries separating usable space from unusable space that are already identified (e.g. land vs. water, forest vs. non-forest) then PHRE may be the more effective method.

Sample size requirement

Depending on methods and species, home range estimates require sample sizes from 18 (Rose 1982) to 1,000 (Boyle et al. 2009). For many species direct field observation is the only available approach for tracking space use, as satellite tags are only effective for wide ranging species (locations are of limited accuracy) and can be prohibitively expensive. As collecting sighting data using radio telemetry is labor intensive, requiring relatively few sighting locations is a desirable trait for a method that is applicable across systems. We found moderate differences in sample size requirements across methods. KDE and LoCoH required a median of 50 and 40 points respectively for home range area to approach an asymptote, whereas PHRE only required 10 points. Achieving stabilization of variance estimates required a larger sample size, approximately 210 sighting locations for all three methods. Note that when applying any of these methods to a new dataset, the exact sample size at which average home range area stabilizes depends on the distribution of sighting locations, so any estimate of sample size requirements will likely be system or species specific. In addition, our estimates of sample size requirements were made relative to a baseline of 300 sighting locations, which reflected sample sizes for animals that were well sampled over a two-year period in our study. Although this analysis indicates that the methods perform well at low sample sizes, we note that these sample size requirements only pertain to asymptotic estimates of area contained, and not to accuracy of home range shape and location. Thus, although lower sample sizes are required by PHRE to estimate the area enclosed within the home range boundary, this does not mean that home range shape and location are also stable at these lower sample sizes.

Predictive accuracy of probability estimates

An accurate method of home range estimation can identify and therefore predict both used and unused locations. Calculating the AUC for each method revealed that KDE predicted the location of presence and pseudo-absence data with the most accuracy (though only marginally better than PHRE). This result was somewhat surprising, as KDE performed the worst in the overlap test, so we expected that the method would suffer from low false positive rates (indicating inclusion of unused areas). We can reconcile this difference by reviewing how the "pseudo-absence data" were produced in the AUC analysis. Because pseudo-absence points were drawn randomly from any location within 1 km of the sighting locations, the absence data fell on both water and land. This fact leads to the somewhat paradoxical result that the KDE home ranges had the highest rate of exclusion of pseudo-absence points, because they were able to exclude both marine *and* terrestrial points. This highlights the fact that the AUC comparison should be qualified by the “exclusion of unusable space” comparison, as poor performance on the latter metric actually allowed for better performance on the former.

Of the three methods tested, PHRE was most successful at excluding unused areas, required the fewest sighting locations, and had high predictive accuracy. However, PHRE also comes with the challenge of obtaining both habitat data and determining species habitat requirements a priori. The preferred method for a given species will thus depend on habitat complexity at the scale of animal space use (to the degree that it influences the risk of type I and II error), availability of sighting data (Fieberg and Börger 2012), availability of environmental data, and the degree to which researchers can identify habitat requirements a priori. For an animal in a relatively unrestricted, simple landscape, such as an African buffalo (*Syncerus caffer*) on a plain with uniform, high quality foraging opportunities (Winnie et al. 2008), there is little risk of including unused areas (type I error), so KDE or LoCoH are preferred as they do not require habitat data. Although there is a risk of excluding used areas (type II error), LoCoH can be useful for describing home ranges in species that encounter moderately complex boundaries, such as white-faced capuchins (*Cebus capucinus*) in forested areas that avoid large clearings and grasslands (Campos and Fedigan 2009), and have incomplete or coarse habitat data available. For species that inhabit a restricted and complex environment with a high risk of incorrectly including unused areas in home range boundaries, such as black bears (*Ursus americanus*) that avoid circuitous roads (Brody and Pelton 1989), northern pike (*Esox lucius*) in riverine habitats (Knight et al. 2009), and Arctic foxes in oil-developed areas with 50% of the land surface covered by water (Eberhardt et al. 1982), PHRE provides a powerful new method for creating estimates that exclude these unused areas. PHRE should perform well in both aquatic and terrestrial environments and for other movement types (such as central-place foragers, where distance from the nest or den site could be included as an environmental feature), but this remains to be tested.

In addition to excluding unused areas and requiring few sighting locations, PHRE allows researchers to evaluate the fit of home ranges estimated using multiple habitat features. As PHRE can be performed in multi-dimensional space, alternative models incorporating different habitat variables can be tested against each other. For example, we found that sea otter home ranges predicted by coastal position and water depth were equally or more accurate than those predicted by coastal position and offshore distance (AUC using depth = 0.98 ± 0.01). In these endeavors, it is useful to have at least one feature that is grounded in geographic coordinate space with 1:1 mapping (e.g. distance along a boundary). Note that as more dimensions are added, alternative methods may be required to select the smoothing parameters (Sain et al. 1994). When using more than two dimensions, we found that the reference smoothing parameter in the ks package provided a good visual fit to the data. By calculating the AUC, researchers can compare the accuracy of multiple models (Walter et al. 2015) that incorporate different habitat variables and choose those that are most biologically appropriate for their study species. While not a substitute for a habitat selection analysis, PHRE could serve as a superior null model in Horne et al.'s synoptic model (Horne et al. 2008), which would allow for subsequent interpretation of habitat selection.

An Ecological Application

In applying PHRE to test the effect of habitat structure on home range shape, we expected that site bathymetry (a proxy for the distribution of accessible resources) would influence sea otter space-use. In support of our hypothesis, analyses showed that for a given home range area, length was greater in Big Sur than in Monterey Bay. Big Sur home ranges were therefore more elliptical overall, and this difference in home range length between sites increased as overall size increased. Mirroring their narrower continental shelf, Big Sur sea otters are only able to increase benthic foraging area by extending their home ranges farther along the coastline. In contrast, Monterey Bay sea otters are able to access shallow offshore resources, and thus can increase home range area by extending their home ranges farther offshore.

Differences in habitat and home range shape have implications for sea otter health, as home ranges of equivalent area are up to 8.47 km longer in Big Sur compared to Monterey Bay. Home range shape may influence risk of exposure to terrestrial pollutants, including zoonotic protozoan pathogens such as *Toxoplasma gondii*, which may be transported into marine ecosystems via sewage systems and freshwater runoff (Miller et al. 2002, Fayer et al. 2004). Encountering longer stretches of coastline in Big Sur may increase exposure to freshwater outputs from multiple watersheds and increase risk of encountering terrestrial pollutants for individual sea otters. In addition, otters with similar home range lengths are expected to realize up to a 37% loss of foraging habitat in Big Sur compared to Monterey Bay. While these restrictions could be offset by higher prey density in Big Sur, recent work on sea otter body condition and foraging success suggests that prey resources are equally or less abundant in Big Sur as compared to Monterey Bay (Tinker et al. *in review*).

The effect of habitat structure on home range shape has implications for costs and benefits of home range use across habitats. It is therefore important to note that the effect of site on home range shape was most detectable using PHRE. KDE, the method used in previous publications that define sea otter home ranges (Tinker et al. 2008a, Larson et al. 2013), showed a difference between sites of lower magnitude and less significance (Figure 2.6). Similarly, the effect size detected using LoCoH was half that of PHRE. Using PHRE to detect differences in home range shape will allow researchers to better evaluate space use trade-offs for species in complex habitats, such as sea otters. Accurate estimates of home range shape and location were previously unavailable for many species in restricted habitats; PHRE fills this niche, and has potential applications for research on exposure to anthropogenic disturbances, encounter rates with pathogens, and access to resources.

Conclusion

PHRE performed well in the coastal environment by successfully excluding unused areas from home range polygons, displaying low sample size requirements, and creating probability estimates with high predictive accuracy and low bias (minimizing both type I and II errors). This method is applicable to ecological studies of species whose home ranges are restricted by complex boundaries or across environmental gradients. Limitations to this method include the need for environmental data and a priori knowledge of habitat features that influence animal space use. In systems for which these requirements are met, PHRE can provide more accurate home range estimates for species in restricted habitats than previous methods, leading to more realistic characterization of the physical and biotic environments with which an individual interacts. Increased accuracy in defining home ranges will allow researchers and resource managers to better understand habitat use requirements and ultimately improve conservation efforts for a variety of species.

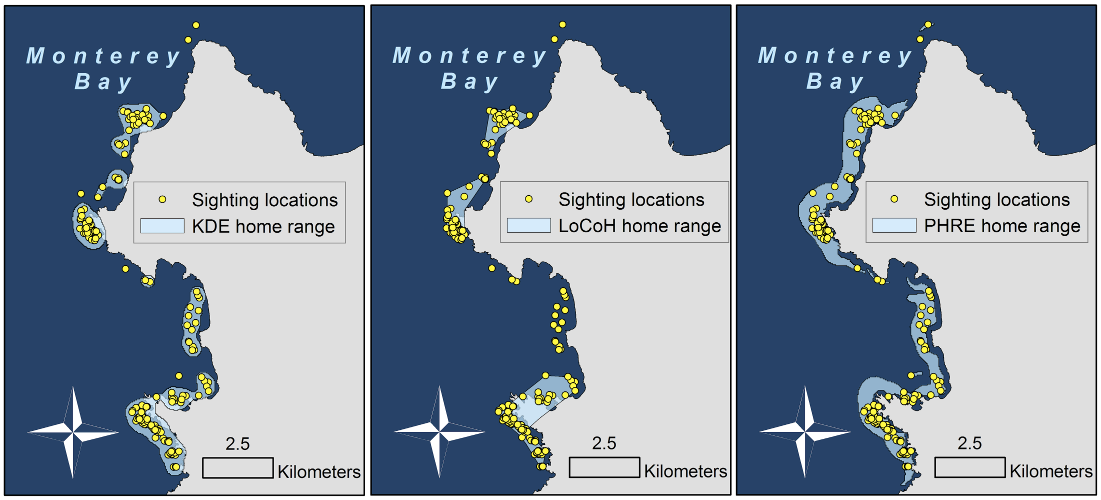

Figure 2.1. Home range polygons estimated using three different methods. The polygons represent the 90% probability isopleth of sea otter number 1392, a female in Monterey Bay, CA. Note the overlap between home range polygons and land for LoCoH (middle; 17% of the home range overlapped with land) and KDE (left; 10%), but not for PHRE (right; 0%).

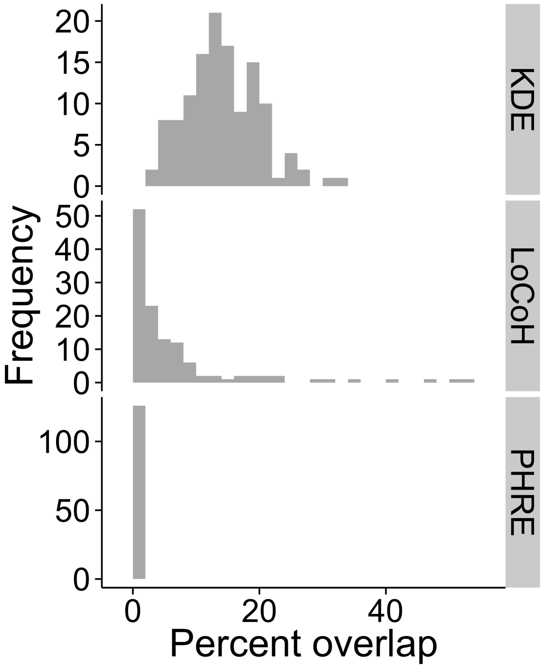

Figure 2.2. Frequency distribution of the percent of home range area that overlapped with land for each method. We calculated the percent of the 90% probability isopleth that overlapped with land (*N* = 126 sea otter home ranges for each method). Three methods are compared: KDE (top), LoCoH (center), and PHRE (bottom).

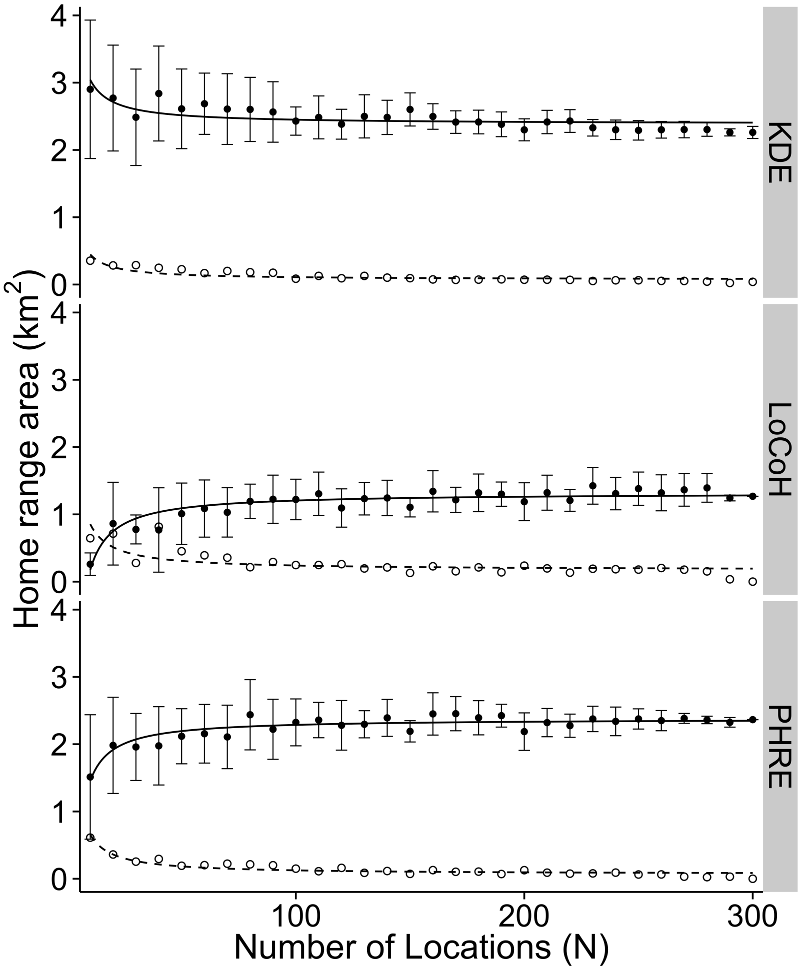

Figure 2.3. Average (± SD) home range area and the coefficient of variation across sample sizes of sighting locations. Home range estimates were iterated 10 times across each sample size for 26 different animals (data for only one animal shown, ID = N-1225-03-S). Closed circles show home range area and open circles show the coefficient of variation. The solid lines denote the asymptotic curves for the data and the dashed lines denote the asymptotic curves for the coefficients of variation. Three methods are compared: KDE (top), LoCoH (center), and PHRE (bottom).

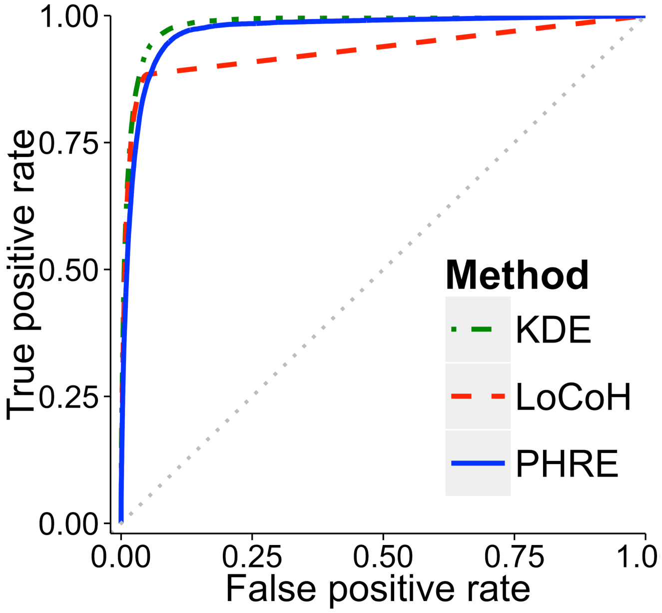

Figure 2.4. Receiver operating characteristic curves comparing predictive accuracy of KDE, LoCoH, and PHRE. Sighting data from 26 animals were used to generate home range estimates (200 random points were selected for ten iterations). For each iteration 100 presence and 1,000 pseudo-absence data were generated to calculate the area under the curve (AUC). Plotted curves show composite estimates for all iterations. Calculated curves can be compared to the grey dotted line, which denotes an AUC of 0.5 where presence and absence predictions are no better than chance.

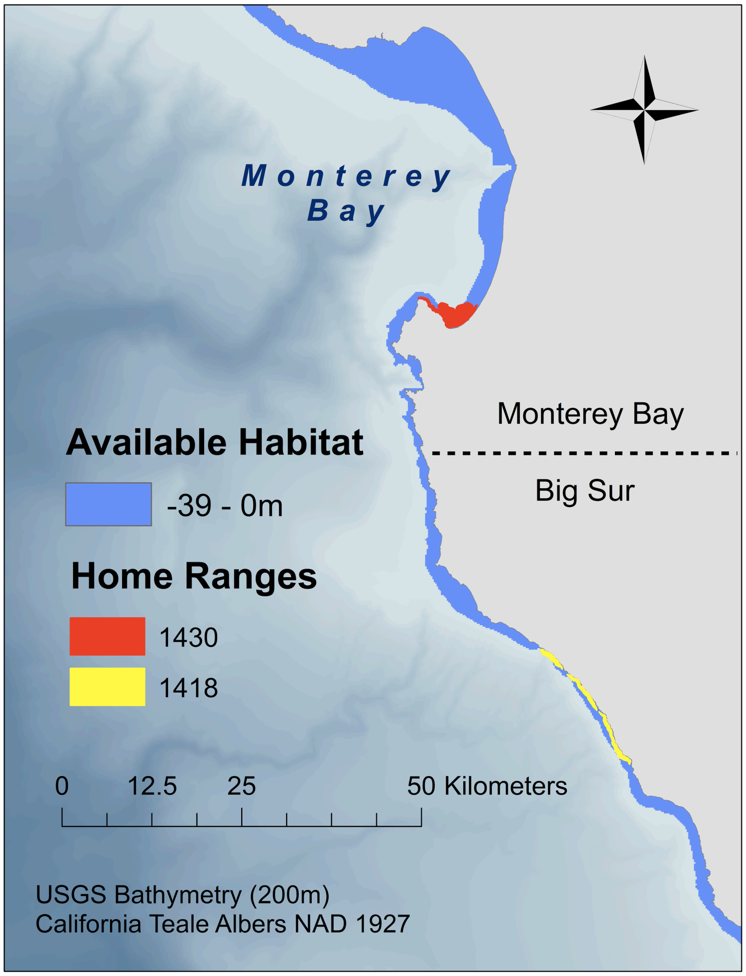

Figure 2.5. Map of available habitat at the Monterey Bay (north of Garrapata State Park) and Big Sur (south of Garrapata State Park) study sites. Because habitat available to foraging sea otters (between 0 and −39 meters depth) extends farther offshore in Monterey Bay, there is greater opportunity for sea otters to increase home range area and access to resources by extending home ranges offshore. In contrast, sea otters in Big Sur are forced to extend their home ranges along the coastline to access more resources. Characteristic home ranges for females at each study area are shown in red (Monterey Bay) and yellow (Big Sur).

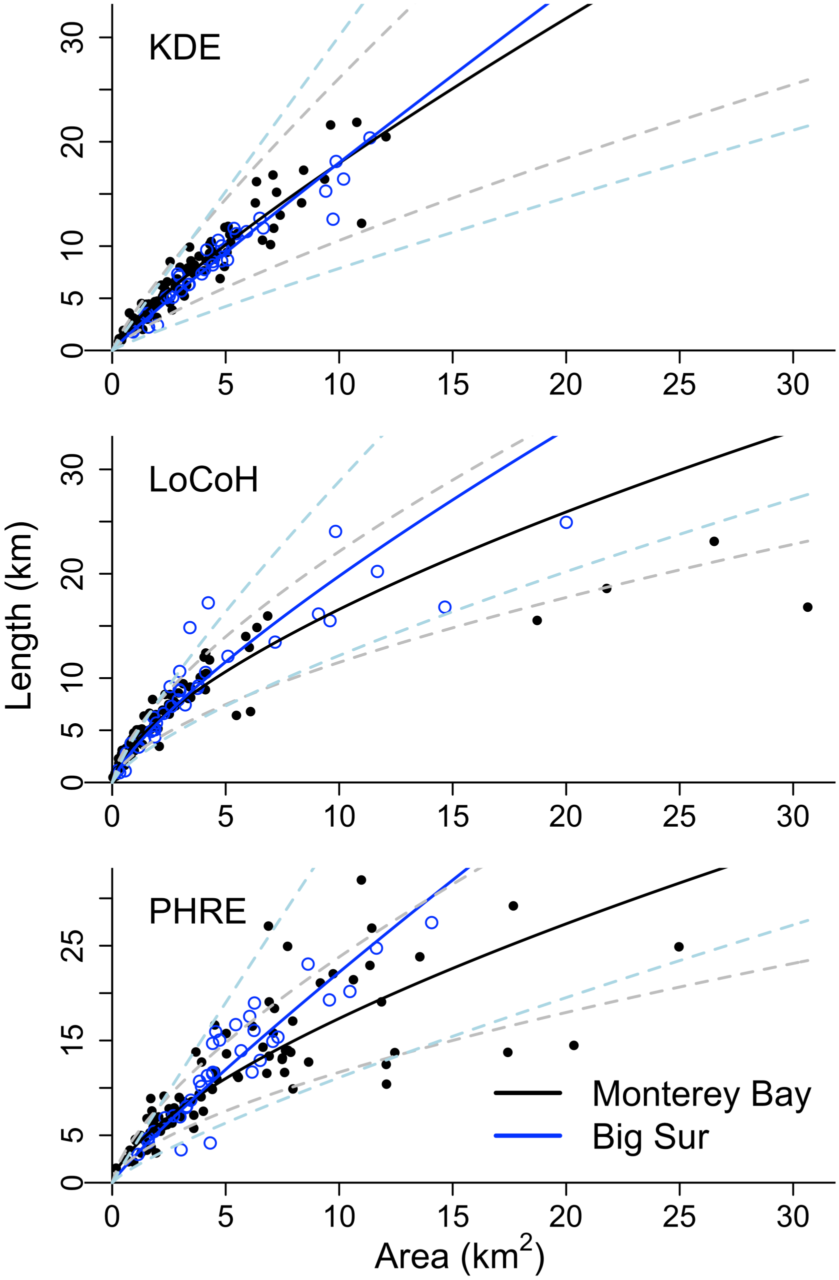

Figure 2.6. Home range length (km) plotted as a function of area (km^2) for otters at two sites in central California. Data represent values obtained from home range estimates created using KDE (top), LoCoH (middle), and PHRE (bottom). Solid, black points represent Monterey Bay ($N = 92$) and open, blue points represent Big Sur ($N = 34$). Fitted power functions are shown by solid lines, with standard error shown by lighter dashed lines. Length increased more rapidly with home range area for sea otters at Big Sur compared to Monterey Bay (i.e. Big Sur home ranges were more elliptical).

Chapter 3

Genetic analysis of reproductive variance in polygynous species and a sea otter case study

Abstract

In polygynous mating systems, reproductive success varies across males because some males monopolize mates that aggregate around patches of resources. Parturition sites act as a resource for female pinnipeds and their stability influences reproductive variance across males. Females aggregate on stable beaches, so terrestrially breeding species such as elephant seals attain high variance in male reproductive success. Aquatic breeding provides little opportunity to monopolize females, so species such as harbor seals have low reproductive variance. Sea otters provide an intriguing test of this framework because they share the marine environment with pinnipeds but evolved from an independent lineage. Sea otters mate aquatically, but male defense of stable aquatic territories suggests moderate polygyny. We quantified male reproductive success from 1998–2011 in Monterey, CA by applying 37 newly developed microsatellite markers to tissue samples from 183 pups, 205 females, and 67 males. Paternity analyses identified 26 father-pup pairs in CERVUS with 95% confidence. To eliminate biases in estimated reproductive variance arising from incomplete sampling of parents and offspring, we constructed a Bayesian model to identify the most likely distribution of male reproductive success given our sampling protocols. We compared reproductive variance across male sea otters, southern elephant seals, and Pacific harbor seals using published paternity data and model outputs. Reproductive variance in male sea otters was below that of elephant seals, but surprisingly elevated above that of harbor seals. The circumstances that enable some male sea otters to elevate their reproductive success despite mating in the aquatic environment merit further investigation.

Introduction

Mating systems emerge as a result of individuals competing to maximize their lifetime reproductive success (Bradbury and Vehrencamp 1977, Clutton-Brock and Harvey 1978, Rubenstein and Wrangham 1986, Dunbar 1988, Reynolds 1996). Mammalian females often maximize reproductive success by investing resources in parental care, whereas males maximize reproductive success by competing for access to females (Trivers 1972, Kiyota et al. 2008). Emlen and Oring (1977) described the role of the environment and resource distribution in the opportunity for males to monopolize females in polygynous mating systems. Scare and evenly distributed resources provide little opportunity for polygyny, whereas abundant resources distributed in patches elevate the environmental potential for polygyny. High environmental potential for polygyny affords males the opportunity to increase their reproductive success and can lead to high variance in reproductive success across males.

High environmental potential for polygyny only translates to reproductive variance across males if males are able to capitalize on the opportunity to monopolize multiple females. Male ability can be constrained by phylogenetic history. For example, most avian species require biparental care to successfully rear offspring, so males are constrained to monogamy, at least in the sense of social monogamy (Burley and Johnson 2002). The degree of polygyny and reproductive variance are therefore shaped by an interaction between the environment and phylogenetic constraints.

The degree of polygyny among carnivoran marine mammals (i.e. pinnipeds) is largely determined by environmental characteristics of the breeding site (Stirling 1983, Le Boeuf 1991). When females haul out to give birth on solid, stable substrate (i.e. land), males can defend multiple females and a high degree of polygyny ensues. This spatial aggregation and synchronous estrus in pinnipeds is facilitated to some degree by the ability of females to rely on fat reserves and geographically disassociate foraging and breeding. When females are more dispersed on unstable substrate (e.g. pack ice), the opportunity for polygyny is lower. Pinnipeds that mate aquatically have particularly low variance in male reproductive success because females are highly mobile in the aquatic environment so are more difficult to monopolize (Coltman et al. 1998, Fabiani et al. 2004, Harcourt et al. 2007).

Sea otters present an intriguing case study to further mating system theory in carnivores. Sea otters share the marine environment with other carnivoran marine mammals, but they are phylogenetically more similar to terrestrial carnivores (Koepfli et al. 2008) and evolved as an independent lineage from pinnipeds. The distribution of estrous females in time and space provides insights into the environmental potential for polygyny in sea otters. Sea otters spatially segregate by sex, with groups of bachelor males resting and foraging in areas that are geographically distinct from females (Garshelis et al. 1984, Jameson 1989). Juvenile dispersal is typical of polygynous mammals, with males dispersing much farther than females (Jameson 1989, Ralls et al. 1996). As adults, some males defend small aquatic territories and females have larger home ranges that encompass multiple male territories (Jameson 1989). Although sea otters live at high densities (2.5 otters/km^2 in central California and 5.7 otters/km in Monterey, CA) (Tinker et al. 2008a, 2012) compared to terrestrial carnivores of similar size, females give birth aquatically so do not form breeding aggregations. Pups are born in every month and sea otters breed throughout the year (Barabash-Nikiforov 1935, Fisher 1940, Murie 1940, Kenyon 1959, Lensink 1962, Sinha et al. 1966, Riedman et al. 1994), with some evidence for peaks in breeding activity (Lensink 1962, Sinha et al. 1966, Riedman et al. 1994). Low synchrony in female estrus may be related to energetic requirements. Sea otters are extreme income strategists so are unable to dedicate time exclusively to reproduction (Thometz et al. 2014); their feeding, resting, and mating activities overlap in time and space. Estrus females are therefore dispersed in time and space. Based on existing mating system theory developed for pinnipeds, sea otters are expected to exhibit a low degree of polygyny and low male reproductive variance because females are dispersed and mating occurs in water.

The genetic mating system of sea otters has never been characterized, so our first objective was to quantify reproductive success and reproductive variance in male sea otters. We accomplished this objective using microsatellite and paternity analyses of tissue samples collected during a 14-year study in Monterey, CA. We then compared reproductive variance of sea otters and two other carnivores that share their habitat: southern elephant seals and Pacific harbor seals. Females in all three species are limited to weaning one pup annually (Sinha et al. 1966, Spotte 1982, Le Boeuf and Reiter 1988, Riedman et al. 1994). Female elephant seals (both the northern and southern species) haul-out in large aggregations for parturition and pup-rearing, so the environmental potential for polygyny is high and the system is characterized by a high degree of polygyny (Bartholomew 1970). There is fierce competition between males for breeding status. Males can maintain alpha status for no longer than three years, and die within a year or two after their reproductive peak (Le Boeuf 1974). Harbor seals mate in water, a trait which strongly limits the environmental potential for polygyny (and thus reproductive variance) in aquatically mating pinnipeds (Coltman et al. 1998, Fabiani et al. 2004, Harcourt et al. 2007). These pinniped species represent two ends of a polygyny continuum.

Studies of genetic mating systems are often limited to short durations with incomplete sampling of adults and offspring (Coltman et al. 1998; Gemmell et al. 2001; Hayes et al. 2006; Pörschmann et al. 2010, but see Le Boeuf & Reiter 1988; Korpimäki 1992; Kruuk et al. 1999), which makes it difficult to compare estimates of lifetime reproductive success across species. While short-term studies are easier to implement, reproductive variance in the short term may not equal variance across lifetime reproductive success. Male reproductive success is often state-dependent and relies on age or mating tactic (Lidgard et al. 2005). When female mate choice plays a role in male mating success, changes in female preference through time make long-term reproductive success less predictable from short-term data (Chaine and Lyon 2008). The effects of incomplete sampling of parents and offspring on estimated reproductive variance are unclear. Low sampling intensity may have an effect similar to low species fecundity, which is known to cause overestimates in reproductive variance (Tsuji and Tsuji 1998).

To address common limitations in study design, our second objective was to deliver a method that estimates variance in lifetime reproductive success based on genetic datasets with incomplete sampling. We used a Bayesian approach inspired by Mobley & Jones (2013) to estimate variance in lifetime reproductive success using short-term data with incomplete sampling of parents and/or offspring. We applied this approach to the genetic mating system of sea otters (characterized in this study) and published paternity data for southern elephant seals and Pacific harbor seals.

Methods

Sea otter reproductive success

Sample collection

We collected blood and tissue samples from live captured and stranded sea otters in Monterey Bay, CA (36.6183° N, 121.9015° W) from 1998 to 2011 (Figure 3.1). SCUBA divers with rebreathers captured wild live otters (N = 212) using Wilson traps (Ames et al. 1986) for tagging (Williams and Siniff 1983) and ongoing behavioral studies (Tinker et al. 2008b, 2012, Johnson et al. 2009, Lafferty and Tinker 2014, Elliott Smith et al. 2015). Additional samples (N = 67) were collected from live and fresh-dead stranded sea otters recovered by the Southern Sea Otter Stranding Network (Estes et al. 2003, Tinker et al. 2016). Collected samples included whole blood preserved in ethylenediamine-tetraacetic acid (EDTA) (N = 58), flipper plugs (5 by 5-mm tissue samples taken from the hole created during application of color-coded plastic tags in the hind flippers) preserved frozen or in 100% ethanol (N = 75), plucked hair (N = 45), buccal swabs (N = 29), muscle stored in cryotubes (N = 7), and other unspecified tissues (N = 65). Tissues were collected using standardized protocols (Tinker et al. *in review*; Kreuder et al. 2003) and stored at −20 to −80°C prior to DNA extraction.

We sampled 67 males and 212 females. Most animals were adults during sampling (269 out of 279). Adult females at the site were likely sired by local males because female juvenile dispersal is limited (Tinker et al. 2008b). The same is not true of males; male juvenile dispersal is extensive (Tinker et al. 2008b). We were more likely to sample the fathers of local adult females than males, so we considered only females as candidate pups. Females comprised 205 candidate mothers and 183 pups, with the possibility for individual females to be both candidate mothers and pups over the course of the 14-year study period. We identified repeat captures and strandings in the field using color-coded plastic flipper tags (Temple Tags, Temple, TX, USA) and sub-cutaneous passive integrative transponders, or “PIT” tags (Yeates et al. 2007). Duplicate samples were removed for paternity analyses.

We estimated pup cohort size and the population of sexually mature males and females for each year by combining annual population counts (Tinker and Hatfield 2015) with an age-structured population matrix model (Tinker et al. 2006b, 2008b), based on the assumption that age/sex structure was well approximated by the stable stage distribution predicted by the model. From these data we estimated our sampling effort as approximately 24% of female pups, 34% of candidate fathers, and 36% of candidate mothers across the fourteen-year study (Table 3.1). Estimates reflect populations within the sampling region from Capitola to Point Lobos (Figure 3.1).

DNA extraction and microsatellite typing

We extracted whole genomic DNA using the DNeasy Blood & Tissue Kit (QIAGEN, Valencia, CA, USA). We employed primers for 39 nuclear microsatellite loci; 24 primers were newly developed for sea otters (Lam *et al. in press*) and 15 were available for sea otters and other lutrines (Table 3.2). We separated PCR products with ABI PRISM 3730 DNA Analyzer (Applied Biosystems Inc., Foster City, CA, USA) and visualized them using STRand version 2.3.69. We denatured capillary solutions of 1 uL of 1:10 dilution of PCR product and deionized water, 0.05uL GeneScan 500 LIZ Size Standard, and 9.95 uL HiDi formamide (Applied Biosystems Inc.) at 95°C for 3 minutes. We included both negative (all reagents except DNA) and positive (well-characterized sea otter DNA) controls in each PCR run. We scored duplicate or triplicate runs for heterozygous and homozygous loci respectively.

Paternity analyses and reproductive success

We conducted paternity and maternity analyses simultaneously and allowed matching of trios (pup, sire, dam). We corroborated parentage assignments using two programs that employ a maximum likelihood approach to parentage: CERVUS (Kalinowski et al. 2007, 2010) and FRANz (Riester et al. 2009). We tested for Hardy-Weinberg equilibrium and estimated exclusion probabilities in CERVUS. In both programs we specified: (a) the typing error rate for alleles (0.01), (b) the proportion of candidate fathers sampled (0.34), (c) the proportion of candidate mothers sampled (0.36), (d) the age of first reproduction for females (3 years) (Riedman et al. 1994) and males (5 years) (Green 1978), and (e) the allele frequencies based on all genotyped samples (N = 279).

The two programs differ in how they identify candidate parents for each pup; CERVUS allows the user to input a restricted set of candidate parents for each pup and FRANz uses estimated birth and death dates to identify candidate parents (Riester et al. 2009). We estimated sea otter age during captures and necropsies based on established tooth-wear and morphological protocols, augmented in most cases by estimates derived from tooth cementum analysis (Garshelis 1984, Bodkin et al. 1997, Kreuder et al. 2003). We then identified candidate parents as any animals that reached reproductive age prior to conception (200–244 days before birth) (Larson et al. 2003). We calculated parentage assignments at the 80 and 95% levels of certainty in CERVUS, and ultimately used a conservative approach to parentage assignments by requiring a consensus across both programs at the highest level of certainty for CERVUS (95%).

Estimating reproductive variance in polygynous species

Carnivore reproductive success

We compared the genetic mating systems of sea otters and two additional carnivore species with published paternity data. We selected southern elephant seals (*Mirounga leonina*) as a reference for strong polygyny and Pacific harbor seals (*Phoca vitulina richardsi*) as a reference for weak polygyny. Fabiani et al. (2004) provided paternity data and sampling protocols for southern elephant seals at a colony in the Falkland Islands. Fabiani et al. (2004) collected tissues samples from 115 pups in 1996, 77 pups in 1997, and 46 total males. This sampling constituted 43% of breeding males and 54–90% of pups from each harem at the colony (we assumed that 72% of pups were sampled). Thirty-two percent of male southern elephant seals survive to reproductive maturity at five years of age, 14% survive to reproduce at age eight (Carrick and Ingham 1962), and maximum lifespan is 20 years (Arnbom et al. 1992). We constructed a survivorship curve using these data and estimated that the average reproductive lifetime for Southern elephant seals was four years. This short reproductive lifetime aligns with reports that male Northern elephant seals die within a year or two after their reproductive peak (Le Boeuf 1974).

Hayes et al. (2006) provided paternity data and sampling protocols for Pacific harbor seals in Monterey, CA. Hayes et al. (2006) collected samples from 70 males and 136 pups in 1997–2000, which constituted 50% of the breeding males and 30% of the pup cohort each year. Male harbors seals reach sexual maturity at 3–7 years of age (Atkinson 1997), and males can live to a maximum of 20–25 years (Thompson and Härkönen 2008). Annual male survival was 0.879 between the ages of 3–7 years in Alaska (Hastings et al. 2012). We constructed a survivorship curve from these data and estimated that the average reproductive lifetime for Pacific harbor seals was five years. This estimate aligns with observations by Hayes et al. (2006) that a male harbor seal attained a reproductive lifespan of at least six years at the study site in California.

Both manuscripts provided frequency distributions of paternity assignments, which we used to determine the reproductive success of individual males. Male southern elephant seals were assigned up to 32 pups in a single year. Male Pacific harbor seals were assigned a maximum of two pups in a given year, and a maximum of four pups across two years (at the 80% confidence level). When the identity of males was not apparent, we assumed that paternity assignments were independent across years, which led to a conservative estimate of the number of paternities per male across years.

Estimated reproductive variance

Reproductive variance is difficult to estimate across lifetime reproductive success because studies nearly always involve incomplete sampling of parents and/or offspring. Meaningful estimates of reproductive variance that allow for comparisons across species require accounting for these “filters” in detecting siring events, so the underlying distribution of reproductive success across males can be estimated. We employed a Bayesian model to estimate the underlying distribution of male reproductive success (and subsequently reproductive variance) given the data and sampling procedures.

In the context of this study, reproductive variance is measured by two indices: (1) the standardized variance in lifetime reproductive success (Wade and Arnold 1980, Arnold and Wade 1984), given by $\sigma_{LRS}^2/\bar{x}_{LRS}^2$, where σ_{LRS}^2 is the variance in lifetime reproductive success and $\bar{x}_{LRS}^2$ is the squared mean lifetime reproductive success of all adult males, and (2) S_3 (Pamila and Crozier 1996), or the effective number S (Nonacs 2000), given by $\frac{n-1/\sum p_i^2}{n-1}$, where n is the number of males and p_i is the proportional contribution of the ith male to the total number of siring events. The approach described in this paper requires the following data: (1) the proportion of individuals sampled from the population, (2) the reproductive lifetime of the species, and (3) paternity assignments.

The Bayesian model generates hypothetical distributions of male reproductive success and associated variance and maximizes the probability of obtaining the observed parentage data given the sampling protocols. Estimates of reproductive variance are ultimately obtained using simulated values of variance in lifetime reproductive success and 95% confidence intervals. This approach was modified from a technique to produce unbiased estimates of reproductive variance from samples with missing offspring and parents (Mobley and Jones 2013). Mobley and Jones (2013) developed this technique to estimate the opportunity for sexual selection across a single cohort of sex-role-reversed pipefish. This paper expands that approach in a Bayesian framework to estimate variance in lifetime reproductive success from short-duration studies of carnivores with differing longevity.

For each year, the binomial probability of detecting siring events (P) is given by an inverse logit function:

$$P = ilogit(-5 + \beta_1 * p + \beta_2 * m)$$

where p is the proportion of pups sampled and m is the proportion of males sampled in that year. True paternities are given by a Poisson distribution. Observed paternities are given by a binomial distribution with the number of trials equal to the number of true paternities that year and the probability of detecting the paternity in each trial equal to P. Estimated lifetime reproductive success is calculated across each male's reproductive lifetime. Long-term studies allow for estimates of reproductive lifetime for individual males, whereas short-term studies rely on the average reproductive lifetime across males.

We calculated reproductive lifetime for each male sea otter in our long-term study and approximated the population average for elephant seals and harbor seals. Both pinniped studies were short-term, so lacked data on reproductive lifetimes for individual males. Reproductive lifetime was only estimated for males that reached reproductive maturity for all species.

We applied this model to paternity data for sea otters and published paternity data for southern elephant seals (Fabiani et al. 2004) and Pacific harbor seals (Hayes et al. 2006). We compared estimated reproductive variance across species using the degree of overlap between the 95% confidence intervals. Parametric results appear as mean ± standard deviation and non-parametric data appear as median (quartile 1, quartile 3).

Results

Sea otter reproductive success

All 39 microsatellite primers successfully amplified PCR products, but locus Mvis072 was not polymorphic across our samples and locus Mvi087 deviated significantly from Hardy-Weinberg equilibrium; both loci were therefore excluded from subsequent analyses (Table 3.2) (Marshall et al. 1998). We detected no deviation from Hardy-Weinberg equilibrium in the remaining 37 loci, suggesting a negligible effect of null alleles. Each locus amplified for a minimum of 275 of the 279 individuals sampled, and the mean proportion of loci typed was 0.9965. The mean number of alleles per locus was 3.89, and the average heterozygosity for the 37 loci was 0.4962. Locus D011 was the most informative, with 7 alleles and a polymorphic information content (PIC) of 0.75. The cumulative probability of exclusion for the first parent in the “neither parent known” case was 0.99998 and 0.999995 for the second parent in the “one parent known” case (although only three mothers were known from observations).

Parentage assignments from CERVUS and Franz differed slightly. CERVUS assigned a similar number of parent-offspring pairs to Franz with strict (95%) criteria (26 and 29 paternity assignments respectively), and more with relaxed (80%) criteria (40 and 29 paternity assignments respectively). Both programs correctly assigned all known mother-pup pairs with high confidence (N = 3). There was general agreement between the two programs for assigned father-pup pairs, and only one instance where a pup was assigned different fathers. In all other instances of misalignment, one program assigned a father while the other program assigned no father with confidence. The two programs agreed on 23 paternity assignments (88% of the CERVUS assignments made using strict criteria), which were subsequently used to calculate reproductive success and variance.

We placed 78 sea otters (28% of the animals sampled) in parent-offspring pairs with high confidence. The proportion of assigned sires by CERVUS (0.17) was less than that expected in the CERVUS paternity simulation (0.34) (Table 3.3), and assignments were low overall. The maximum number of pups assigned to an individual male was three, and 81% of males were assigned no pups (Figure 3.2). Among males that sired at least one pup, the mean number of pups assigned was 1.77 ± 0.93.

Estimated reproductive variance in polygynous species

According to Bayesian estimates, male sea otters sired a median of 2 (1,6) surviving female pups across their lifetime (Figure 3.3). The most successful 10% of males sired ≥12 surviving female pups, and the maximum number of siring events exceeds 12 pups. Standardized variance in male reproductive success was 2.44 (0.60, 5.78) for male sea otters (Figure 3.4). The effective number S (S_3) reflects the evenness of the proportional pup contribution by each male, where a value of 0 indicates that all males contribute equally to reproductive output and a value of 1 indicates that one male produced all pups. S_3 was 0.72 (0.38, 0.86) for male sea otters, indicating a moderate degree of polygyny (Figure 3.5).

Sea otters had lower estimated reproductive variance than elephant seals (standardized variance in LRS = 6.54 and $S_3 = 0.88$) and higher estimated reproductive variance than harbor seals (standardized variance in LRS = 1.00 and $S_3 = 0.50$) based on both indices of reproductive variance (Figure 3.4 & Figure 3.5). Fifty percent of male elephant seals sired between zero and two pups across their lifetime, and the most successful 10% of males sired ≥32 pups. Harbor seals showed much lower reproductive success and variance. Fifty percent of male harbor seals sired between zero and one pup, and the most successful 10% of males sired ≥3 pups.

We evaluated model sensitivity using outputs from the sea otter analysis. Parameter estimates for β_1 and β_2 reflect the effect of the proportion of pups and males sampled from the population on the probability of detecting siring events. Parameter estimates that include zero in the 95% confidence intervals indicate no effect, whereas positive parameters indicate a positive effect on detection. Sampling intensity of pups did not affect the probability of detecting siring events ($\beta_1 = -0.02 \pm 0.90$), while sampling intensity of males had a strong positive effect on the probability of detecting siring events ($\beta_2 = 5.10 \pm 0.82$) (Figure 3.6). However, estimated male population size had a negligible effect on estimated reproductive variance. A 50% decrease in our estimate of the proportion of males sampled led to only a 4% decrease in mean estimated reproductive variance (i.e. S_3) and the mean remained within the 95% confidence intervals of the original estimate.

Discussion

Sea otters share the marine environment with pinnipeds but are phylogenetically most similar to terrestrial carnivores. These characteristics make them an interesting case for testing predictions from mating system theory, in particular that marine mammals in the order Carnivora exhibit low variance in male reproductive success if species mate aquatically. Among other marine mammals in the order Carnivora, species that mate in water often exhibit low variance in male reproductive success (i.e. weak polygyny) because males are less successful at monopolizing females in the aquatic environment. Sea otters mate in water, but some males defend reproductive territories, which is a frequent characteristic of moderate to strong polygyny.

Recently developed genetic markers in sea otters (Lam *et al. in press*) offered a method to explore their genetic mating system. Even with genetic data, comparisons between the mating systems of sea otters and other carnivores are complex because studies are often of short duration and only a portion of the population is sampled. Incomplete sampling leads to biased estimates of reproductive variance, and these biases are not consistent across species (Mobley and Jones 2013). Further, variance in lifetime reproductive success indicates the potential for selection (if traits that are correlated with reproductive success are heritable), but it is unclear how well reproductive variance across a limited number of cohorts predicts variance across lifetime reproductive success. We characterized the genetic mating system of sea otters, compared it to the genetic mating systems of other carnivores, and, in the process, formulated a method for estimating variance in lifetime reproductive success from short-term data with incomplete sampling of parents and offspring.

Genetic mating systems of sea otters and other carnivores

Sea otter genetic diversity is low in California due to near extirpation in the 1800s and a subsequent genetic bottleneck (Larson et al. 2002). We overcame the challenge of analyzing relatedness in a population with low genetic diversity by employing markers for 37 polymorphic microsatellite loci (Lam *et al. in press*), which allowed us to assign paternity with high confidence. The cumulative probability of exclusion for the first parent in the "neither parent known" case was 99% and we placed 28% of individuals in a pedigree with high confidence. We assigned 23 father-pup pairs with strict criteria (95% confidence in CERVUS and consensus with FRANz) and 40 pairs with relaxed criteria (80% confidence in

CERVUS). The maximum number of pups assigned to a male was three and the maximum number in a single year was two. Paternity assignments were lower than true siring rates because we sampled: (a) adults, thereby excluding any pups that did not survive to adulthood; (b) females, due to the limited dispersal of females and the high likelihood of a local origin; and (c) a small proportion of the population, the effects of which we explore below with model outputs. This constitutes the first genetic study of male reproductive success in sea otters.

Our genetic analysis supports the characterization of sea otters as polygynous (Riedman and Estes 1990). Among the animals sampled for this study, males produced pups with up to two different females per year whereas females produced a single pup with only one male per reproductive bout (Sinha et al. 1966). Estimated reproductive variance further supports moderate polygyny in sea otters and is higher than estimates in aquatically mating pinnipeds (Coltman et al. 1998, Hayes et al. 2006, Harcourt et al. 2007) (Figure 3.4 & Figure 3.5). This finding goes against our prediction that sea otters have low reproductive variance due to dispersion of females in space and low synchrony in estrus (Emlen and Oring 1977), and does not align with previous findings that monopolizing mating opportunities is difficult in the marine environment (Coltman et al. 1998, Fabiani et al. 2004, Harcourt et al. 2007). It seems that some males are able to effectively monopolize multiple females in their aquatic habitat, and begs the question of how they accomplish this feat.

One clue into how males accumulate paternities may lie in the timing of reproduction. Male sea otters were assigned at most one to two offspring in a given year, suggesting a fairly low potential for polygyny over short time periods. However, some males achieved higher reproductive success by maintaining reproductive activity, which usually entailed defending a mating territory, over multiple years. These findings suggest that sea otters (and potentially other aquatically breeding marine mammals) experience polygyny over time rather than space, where the most successful strategy is to maintain a breeding position and to accumulate paternities over multiple breeding seasons. Low synchrony in female estrus and a prolonged mating season influence the relative importance of time versus space in polygyny (Pörschmann et al. 2010). The pattern of accumulating paternities over time may be particularly important in sea otters because females have low synchrony in estrus.

Such a “long-game” strategy of reproductive success may be imposed on male sea otters by their phylogenetic history and unique physiology. Sea otters are energetically constrained because they are the smallest marine mammal, lack energy stores in the form of blubber, and have elevated metabolic rates (Costa and Kooyman 1982). They are therefore unable to fast for any prolonged period, and must maintain a continuous and high rate of energy intake to survive (Thometz et al. 2014). Sea otters are considered extreme income strategists and their feeding and breeding areas overlap, a characteristic that is unique from most pinnipeds. Even with this overlap of feeding and breeding areas, many territorial male sea otters periodically vacate their territories, moving to “male-dominated” areas to feed and replenish energy stores before returning to their territory after days to months (Garshelis et al. 1984, Jameson 1989, Tinker et al. 2008b, Lafferty and Tinker 2014). During these forays males necessarily miss mating opportunities; however, replenishing their energy stores presumably increases survival to future reproductive events.

In contrast, elephant seals are comparatively massive and fast the entire breeding season while posturing and fighting despite the hefty energetic costs (Galimberti et al. 2007). Elephant seals in the dominant, or alpha, breeding position are unlikely to survive past two or three successful breeding seasons (Le Boeuf 1974) due to their large investment in current reproductive success. This difference in body size has a clear effect on a species' ability to separate breeding and feeding areas and may subsequently affect mating systems. Further exploration of the relationship between body size, fasting ability, and the relative emphasis of polygyny over time versus space would highlight how phylogenetic constraints on body size play a role in mating strategies.

Estimated reproductive variance in polygynous species

Incomplete genetic sampling of parents and offspring complicates estimates of reproductive variance. We made sense of sea otter paternity data by creating a Bayesian model that estimates the underlying reproductive variance from genetic studies with incomplete sampling. We further applied this model to existing data of southern elephant seals and Pacific harbor seals. Our Bayesian model is widely applicable across species because it is generalized for any paternity dataset and requires data that are commonly reported in studies of genetic mating systems. The model inputs comprise: (1) the proportion of individuals sampled from the population, (2) the reproductive lifetime of the species, and (3) paternity assignments. Our model will help researchers design studies of genetic mating systems and interpret paternity data.

Model outputs revealed that sampling efforts should target adult males to detect reproductive variance and polygyny. The proportion of males sampled has a strong effect on the probability of detecting siring events, whereas the proportion of offspring sampled has no measurable effect. For sea otters, β_1, the parameter indicating the effect of the proportion of pups sampled on the estimated number of paternities, was -0.12 ± 0.91, and β_2, the parameter indicating the effect of the proportion of males sampled on the estimated number of paternities, was 5.13 ± 0.80. Mobley and Jones (2013) described a similar effect of sampling in their model for detecting reproductive variance in open populations. If resources limit sampling efforts, efforts should target candidate parents over offspring.

Parameter estimates and confidence intervals make sources of model sensitivity easy to detect. Unlike in Mobley and Jones (2013), estimates of reproductive variance were not particularly sensitive to estimated population size for sea otters. We elevated estimated population size by 50% and found that mean estimated reproductive variance (S_3) increased by only 4% and did not deviate from within the 95% confidence intervals of the original estimate. Our estimates of reproductive variance may be more stable because they are estimated using 12 years of paternity data as opposed to only 1–2 years in many other studies. If model sensitivity is higher for shorter studies, we suggest that users specify error around population estimates and evaluate variance across a range of estimated population sizes.

Model modifications can incorporate nonrandom sampling of parents and age effects on siring. The model estimates the variance in lifetime reproductive success across the sampled males. For this estimate to reflect reproductive variance across males in the larger population, the sampled males must be randomly selected from the population. This is rarely the case because males that share similar siring probability are often clustered in space and/or are more similar in how accessible they are for sampling. The model can account for biased sampling by adjusting the siring probabilities using the relative reproductive success of sampled and unsampled males.

The model can further accommodate species life history and study design. The presented model simplifies siring probability by holding the mean constant across years for each male. The effects of age or other male states (e.g. alternative mating tactic) on siring probability can be added using an additional model term. The model includes sampling of parents and offspring as a “filter” to detecting siring events, and users can add additional filters to paternity assignment.

This model provides a strong option for estimating variance in lifetime reproductive success from genetic studies with short durations and incomplete sampling. This method will allow researchers to leverage existing datasets for comparative work, and to minimize costs in future studies. Application of the model will lead to further insights about the drivers and consequences of genetic mating systems.

Conclusion

This research constitutes the first genetic study of the sea otter mating system. Results confirmed that sea otters exhibit polygyny, and revealed surprisingly high variance in reproductive success across males. These findings contradict the prediction that aquatically-mating marine mammals are less able to monopolize females. Future work should examine the male characteristics and behaviors that facilitate access to females and contribute to this high variance in male reproductive success. In the process of comparing genetic mating systems across carnivore species, we devised a new method to estimate variance in lifetime reproductive success using genetic data from short-term studies with incomplete sampling of parents and offspring. Our Bayesian model handles realistic complications in study design, such as uneven sampling across field seasons, and provides comparable estimates of variance in lifetime reproductive success that will benefit studies of genetic mating systems in multiple taxa.

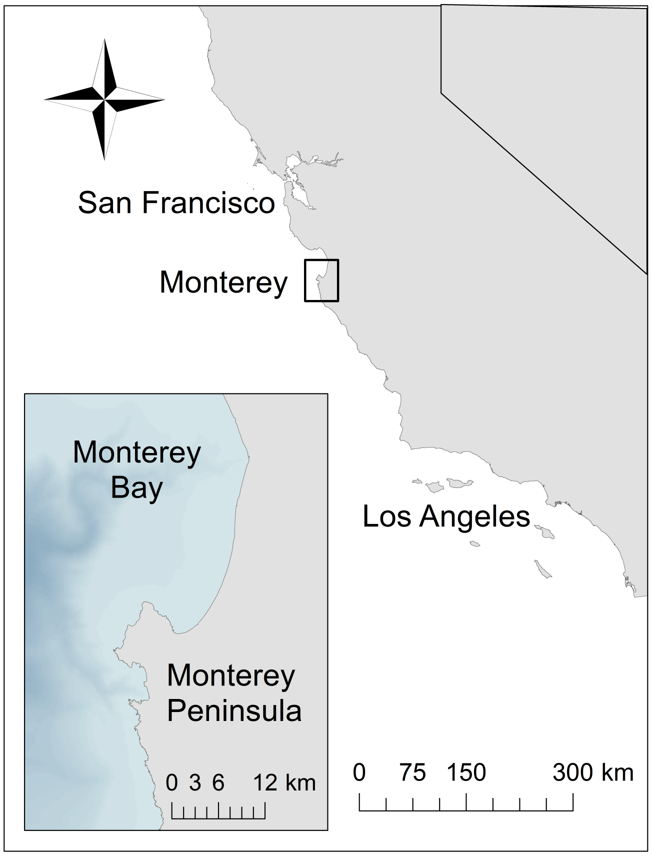

Figure 3.1. Map of the study area in California, USA. The primary study area, Monterey Bay (Capitol to Point Lobos), is enlarged.

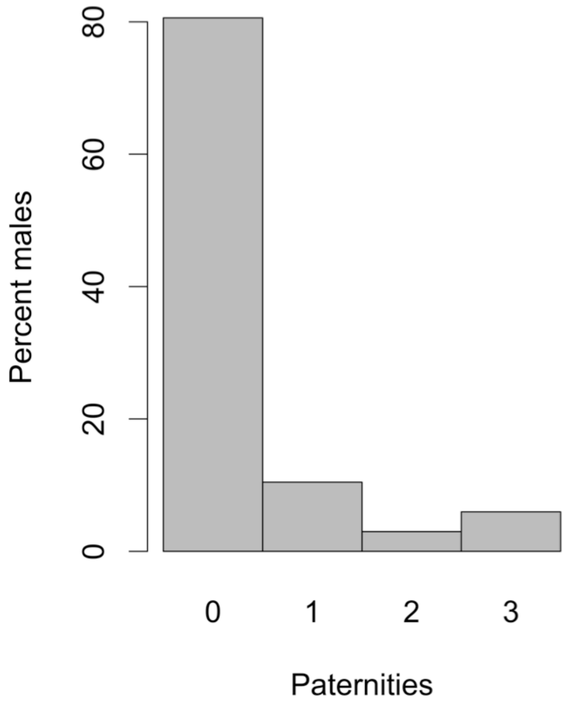

Figure 3.2. Paternities assigned to male sea otters in Monterey, CA from 1998–2011 (N = 67). Eighty-one percent of males were assigned zero pups, and the greatest number of pups assigned to an individual male was three. Paternities were estimated using microsatellite assignment and strict criteria in the parentage programs CERVUS and FRANz.

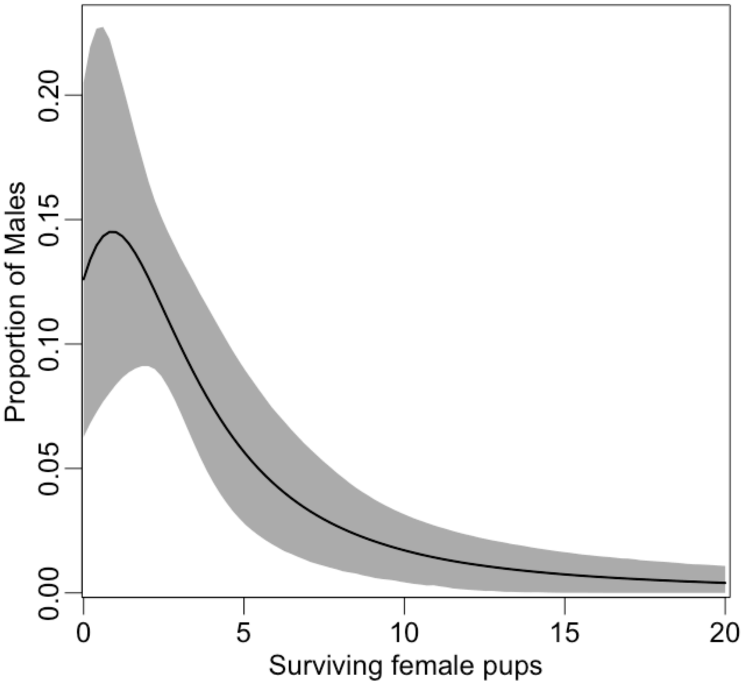

Figure 3.3. Bayesian estimates of variation in siring success across male sea otters. Estimates reflect surviving female pups produced across each male's lifetime. The solid line denotes the mean and shaded areas encompass the 95% confidence intervals.

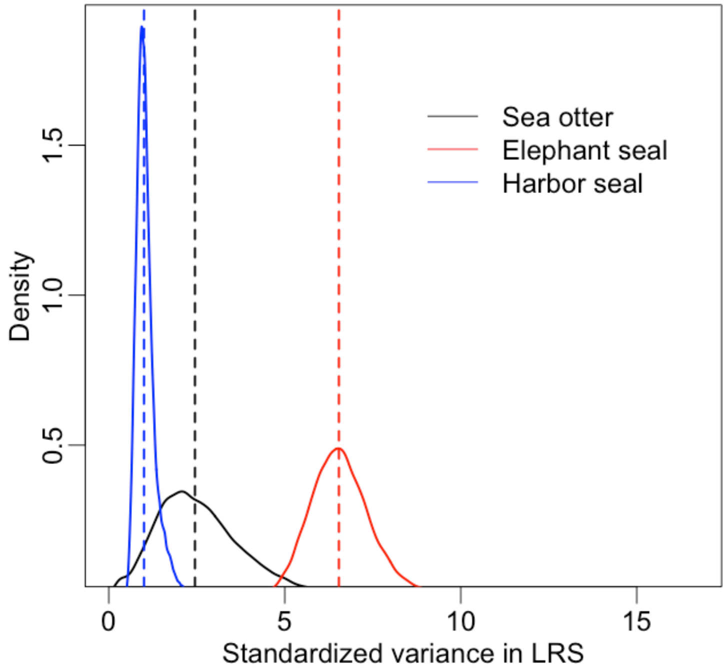

Figure 3.4. Bayesian posterior distributions of standardized variance in lifetime reproductive success across male sea otters. This index is given by the variance/mean^2 reproductive success for all sampled males. Dashed lines denote median values.

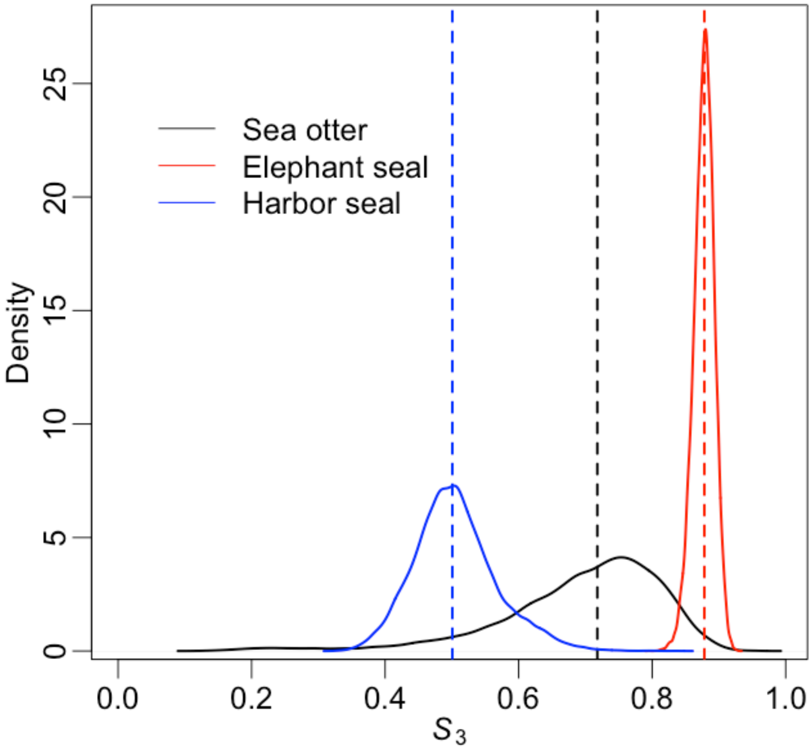

Figure 3.5. Bayesian posterior distributions of S_3 of reproductive variance across male sea otters, southern elephant seals, and Pacific harbor seals. S_3 ranges from 0, when the proportional contribution of pups by each male is equal, to 1, when one male contributes all pups. Dashed lines denote median values.

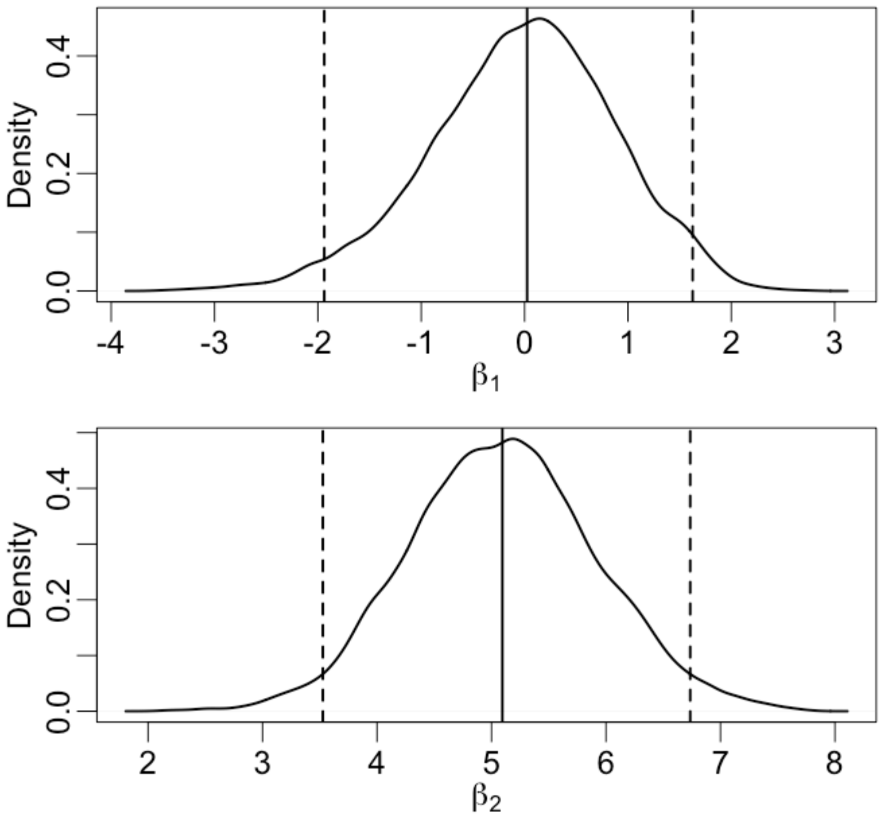

Figure 3.6. Bayesian posterior distributions of β_1 (top) and β_2 (bottom) for sea otters. β_1 indicates the effect of the proportion of pups sampled from the population on the probability of detecting siring events. β_2 indicates the effect of the proportion of males sampled from the population on the probability of detecting siring events. Solid lines denote median values, and dashed lines denote 95% confidence intervals. β_2 differs from 0 and is much greater than β_1, indicating a stronger effect of the proportion of males sampled compared to the proportion of pups sampled.

Table 3.1. Number of sea otters sampled and assigned parentage in Monterey Bay, CA from 1998–2011. Cumulative sample size (cumul. N) indicates the number of unique individuals and the proportion of the population sampled (prop. of pop.) indicates the proportion of the total population sampled across the study period. Population estimates arose from annual census data (Tinker and Hatfield 2015) and an age-structured population model. Paternity and maternity assignments were made using strict criteria (95% confidence in CERVUS and agreement with FRANz).

	Samples			Assignments		
Year	Pups	Adult Males	Adult Females	Paternity	Maternity	Parent pair
1998	14	14	12	0	3	0
1999	7	21	19	0	2	0
2000	32	28	21	2	3	0
2001	27	36	29	2	1	1
2002	32	42	40	3	4	1
2003	20	45	44	2	0	1
2004	13	49	70	0	3	2
2005	12	52	92	0	1	2
2006	12	54	113	1	2	2
2007	7	57	127	1	0	1
2008	2	56	133	0	1	0
2009	4	55	135	1	0	1
2010	0	55	136	0	0	0
2011	1	46	137	0	0	0
Cumul. N	183	67	205	12	20	11
Prop. of pop.	0.24	0.34	0.36	-	-	-

Table 3.2. Description of microsatellite loci used in parentage analysis of California sea otters. Values were calculated in CERVUS, where length (bp) = base pair length, k = number of alleles, N = number of individuals typed, H_O = proportion of heterozygotes observed, H_E = proportion of heterozygotes expected, PIC = polymorphic information content, Exclu. power = probability of exclusion for first parent, and F(Null) = frequency of null alleles. *Loci excluded from parentage analyses due to lack of polymorphism (Mvis072) and deviation from Hardy-Weinberg Equilibrium (Mvi087). References are 1 (Lam et al. *in press*), 2 (Kretschmer et al. 2008), 3 (Dallas and Piertney 1998), 4 (O'Connell et al. 1996), and 5 (Fleming et al. 1999).

Locus	Length (bp)	k	N	H_O	H_E	PIC	Exclu. power	F(Null)	Ref.
EluA011w	205–221	4	277	0.661	0.702	0.646	0.725	0.0318	1
EluA109w	235–249	4	278	0.464	0.436	0.396	0.905	−0.0239	1
EluA202w	252–276	9	278	0.701	0.694	0.65	0.717	−0.0026	1
EluA309w	206–214	4	279	0.427	0.412	0.386	0.911	−0.0138	1
EluA312w	237–241	3	278	0.55	0.572	0.506	0.837	0.0187	1
EluA314w	149–163	4	278	0.511	0.494	0.419	0.876	−0.0191	1
EluA315w	195–215	4	279	0.656	0.686	0.633	0.738	0.0211	1
EluA316w	204–208	3	279	0.541	0.503	0.413	0.874	−0.0368	1
EluA318w	198–212	6	277	0.668	0.63	0.559	0.79	−0.036	1
EluA324w	242–246	3	279	0.602	0.586	0.507	0.829	−0.0109	1
EluA325w	156–172	5	278	0.669	0.685	0.636	0.735	0.0093	1
EluB110w	160–170	5	279	0.688	0.717	0.662	0.711	0.0209	1
EluB118w	231–233	3	279	0.1	0.102	0.097	0.995	0.007	1
EluB122w	206–210	4	278	0.608	0.616	0.534	0.81	0.0069	1
EluB302w	219–227	3	277	0.379	0.366	0.336	0.933	−0.015	1
EluB312w	156–168	6	275	0.596	0.568	0.52	0.825	−0.0297	1
EluB313w	274–282	5	276	0.315	0.339	0.285	0.943	0.0368	1
EluB317w	243–251	3	278	0.493	0.467	0.42	0.891	−0.0354	1
EluB326w	235–245	3	279	0.541	0.552	0.478	0.848	0.0098	1
EluD011w	236–264	7	276	0.699	0.787	0.754	0.593	0.0561	1
EluD119w	232–240	4	278	0.626	0.668	0.593	0.777	0.0313	1
EluD219w	178–186	3	279	0.534	0.538	0.45	0.856	0.0046	1
EluD311w	171–179	3	278	0.518	0.504	0.387	0.873	−0.0136	1
EluD320w	200–212	5	279	0.595	0.59	0.524	0.823	−0.0116	1
Elu001	183–195	3	278	0.284	0.299	0.259	0.956	0.0247	2
Elu003	182–186	2	279	0.165	0.163	0.15	0.987	−0.0052	2
Elu005	134–144	3	279	0.065	0.063	0.061	0.998	−0.0078	2
Elu007	261–265	2	279	0.52	0.482	0.365	0.884	−0.0384	2
Elu009	260–276	3	278	0.525	0.499	0.387	0.876	−0.0278	2
Elu010	132–140	3	277	0.397	0.403	0.353	0.919	−0.0025	2
Lut453	108–112	2	279	0.283	0.306	0.259	0.953	0.038	3

Lut457	180–184	3	278	0.597	0.581	0.513	0.832	−0.0176	3
Lut615	247–281	7	277	0.433	0.491	0.441	0.877	0.0612	3
Lut701	180–188	3	279	0.47	0.483	0.371	0.884	0.0129	3
Lut832	200–204	3	277	0.318	0.32	0.271	0.949	0.0018	3
Mvi057	123–127	3	279	0.473	0.511	0.455	0.87	0.0402	4
Mvis072*	272–272	4	277	0.686	0.692	0.631	0.739	0.005	5
Mvis075	164–170	4	277	0.661	0.702	0.646	0.725	0.0318	5
Mvi087*	88–90	4	278	0.464	0.436	0.396	0.905	−0.0239	4

Table 3.3. CERVUS parentage assignment criteria and assignment rate for sea otters in Monterey, CA. Assignments met criteria for strict confidence (95%).

Assignment Type	Confidence	Critical delta LOD score	Assignment rate observed (expected)
Maternity	95%	4.58	19% (34%)
	80%	1.81	25% (43%)
Paternity	95%	3.06	17% (34%)
	80%	0.00	33% (42%)
Parent pair	95%	9.75	7% (12%)
	80%	6.00	8% (15%)

Chapter 4

Age and kelp affect male reproductive success in southern sea otters

Abstract

In polygynous mating systems, males compete for females. Male quality and competitive ability influence reproductive success. Reproductive success of male sea otters may be related to defense of small territories (2–6 km^2) in shallow coastal waters. To identify the predictors of reproductive success in male sea otters, we used genetics and paternity analysis, along with information on several phenotypic attributes. We characterized space use of VHF radio-tagged males throughout central coastal California and identified territorial and non-territorial tactics. A Bayesian nonparametric proportional hazards model distinguished between the following predictors of siring success across a 14-year study: male attributes, space-use tactics, and territory resources. Among male attributes, age predicted siring success. Males reproduced between the ages of five and 14 years. Siring probability peaked at age seven and remained elevated until age eleven. Both territorial and non-territorial males sired pups, and non-territorial males frequently transitioned to a territorial tactic in subsequent years. Our study supports a mating system characterized by resource defense, where males defend large patches of kelp that offer shelter to females and pups.

Introduction

Polygyny (i.e. the mating system in which males mate with multiple females) arises when males monopolize mates by defending resources or females directly (Emlen and Oring 1977). Polygynous mating systems may manifest as resource defense polygyny, female defense polygyny (Vanpé et al. 2009), or lekking polygyny (Alonso et al. 2012). The use of these strategies depends on the defensibility of females, which is directly influenced by female density, distribution, range size, group size and stability, and indirectly influenced by resource distribution (Clutton-Brock 1989). Mating systems are influenced by both the distribution of resources in space and the distribution of estrous females over time. Synchronous estrus affords greater opportunities for males to mate with multiple females (Emlen and Oring 1977).

Foundational studies of mating systems in pinnipeds support a model for polygyny where males monopolize females that aggregate on terrestrial haul-outs for parturition and pup rearing (Bartholomew 1970). These dense female aggregations allow for extreme polygyny in some species, such as northern elephant seals, where 3% of the males may gain up to 92% of observed copulations (Le Boeuf and Reiter 1988). Not all pinnipeds mate on stable, terrestrial substrate; some mate aquatically (Gemmell et al. 2001, Van Parijs 2003, Kiyota et al. 2008). Aquatic mating may thwart male attempts to monopolize females, lowering the degree of polygyny and reproductive skew—a measure of variance in reproductive success (Fabiani et al. 2004, Harcourt et al. 2007). However, the reproductive success of aquatically mating males is uncertain due to the difficulty in observing and sampling these individuals (Van Parijs 2003).

Sea otters (*Enhydra lutris*) offer an opportunity to study the mating system of a marine mammal where females are not aggregated on stable substrate. Sea otters are the sole carnivoran marine mammal that does not haul out on land for reproduction, and instead engages in aquatic parturition and pup rearing. This characteristic sets sea otters apart from pinnipeds and likely influences the potential for monopolization of females in this species. While male pinnipeds can intercept females as they travel between terrestrial haul-outs and aquatic foraging grounds, the opportunities afforded to male sea otters for monopolizing mates are at present unclear.

Sea otters spatially segregate by sex (Garshelis et al. 1984, Jameson 1989). In female-dominated areas, some males defend aquatic territories and females have annual home ranges that encompass multiple male territories. Sea otters breed throughout the year (Barabash-Nikiforov 1935, Fisher 1940, Murie 1940, Kenyon 1959, Lensink 1962, Sinha et al. 1966, Riedman et al. 1994), with some seasonality in breeding activity (Lensink 1962, Sinha et al. 1966, Riedman et al. 1994). However, this seasonality varies geographically and the peaks are spread over longer periods of time compared to pinnipeds. Pinniped species typically have a short mating season each year, so sexually receptive females are clustered in time. Territorial male sea otters therefore defend territories year-round to capitalize on females that forage, rest, groom, and socialize within these areas and may come into estrus at any time.

Resources that are potentially important to female sea otters include kelp canopy for resting, subtidal benthic habitat rich in invertebrate prey, and areas sheltered from storm events. Previous studies in Alaska indicated that male success in securing copulations is related to age, weight, the length of time the individual maintained the territory, and territory quality, which was ranked based on primarily abiotic features, such as area, depth, and exposure (Garshelis et al. 1984). Although these features influenced copulations, it is unknown whether copulations resulted in paternity and successful reproduction.

Males without territories join bachelor groups or wander throughout the range as transients. Preliminary observations suggest that non-territorial males may be younger and transition to territoriality as they grow older. This hypothesis has not been confirmed with space-use and age data. Although territorial males actively exclude non-territorial males from defended areas, we have observed non-territorial males copulating with females. The reproductive success of males has never been quantified and the importance of male attributes, territory resources, and space-use tactics is unknown.

The objectives of this study were to: (1) describe space-use tactics of male sea otters, and (2) determine the male attributes and behavior that affect reproductive success. This study distinguished male space-use tactics across the southern sea otter range, and measured the effects of individual attributes and territory resources on the reproductive success of VHF radio-tagged males in Monterey, CA. Microsatellite paternity analysis allowed quantification of reproductive success. We predicted that siring probability would increase with higher (a) age, (b) mass, (c) grizzle (the extent of light-colored pelage on the head and body), and (d) heterozygosity, and that territorial males would have the highest reproductive success. The following territory features may predict reproductive success among territorial males: (a) foraging opportunities, (b) kelp canopy availability, (c) shelter availability, (d) territory depth, and (e) territory area. This study reports the significant predictors of reproductive success and characterizes the sea otter mating system.

Methods

Study location

Southern sea otters currently inhabit coastal waters in California, USA from Half Moon Bay to Santa Barbara (Figure 4.1). This study characterized male space use at six sites throughout the range—Monterey, Big Sur, Piedras Blancas, San Luis Obispo, Point Conception, and Santa Barbara—and analyzed reproductive data for a subset of males at the site with the longest history of monitoring (Monterey). Range-wide population survey data were available each spring for the duration of the study (USGS Western Ecological Research Center 2014). Although surveys do not distinguish between adult males and females, the presence of pups is a good indicator of the relative abundance of reproductively active females. Areas with a "pup ratio" ≥ 0.1 pups/independent adults are considered "female-dominated areas."

Genetic sampling efforts occurred on the coast of Monterey Peninsula, CA (36.6844°, −121.9194°), which had the longest history of monitoring and allowed for a 14-year study of male reproductive success (1998–2011). Monterey Peninsula (inset in Figure 4.1) contained two female-dominated areas on the northeast and southwest edges, which spanned 13.5 and 19 km of coastline respectively. Distance was measured "as the otter swims" along the 10m bathymetric contour. Males establish small, sequential territories along the coast in these areas (Loughlin 1980, Jameson 1989). Females (either alone or with a pup) move within overlapping home ranges that encompass multiple male territories (Loughlin 1980).

Non-territorial males are excluded from male territories and either rest in bachelor groups in neighboring male-dominated areas (Loughlin 1980) or wander throughout the California range. The closest notable bachelor group to Monterey Peninsula occurred 23 km to the north at Moss Landing. Territorial males travel periodically to Moss Landing, 94 km south to Big Sur, or farther to the range ends for durations of days to months, and are generally able to reclaim their territory in Monterey upon their return (Jameson 1989).

We collected sea otter tissue samples (described below) during captures at Monterey Peninsula and following stranding events along the 40 km of coastline between north of the Peninsula (36.6336°, −121.8456°) and south of Point Lobos (36.5044°, −121.9420°). Based on annual census-survey data (Tinker and Hatfield 2015) and an age-structured population model (Tinker et al. 2006b, 2008b), the

Monterey study area contained estimates of 42 ± 7 adult males, 199 ± 33 adult females, and 55 ± 9 female pups in a given year during our study (Chapter 3).

Captures: male attributes, genetic sampling, and tagging

We captured sea otters using rebreather SCUBA and Wilson traps (Ames et al. 1986) in the fall and spring throughout the study period (1998–2011), as allowed by logistics and resources. The suite of recorded health parameters for each captured otter included mass, girth, and length (Tinker et al. *in review*). Established tooth-wear and morphological protocols (Garshelis 1984, Kreuder et al. 2003) yielded age estimates. The male's residual mass from the average mass-by-age function (Laidre et al. 2006) (created using male data from Monterey [Tinker et al. *in review*]) provided an age-independent estimate of body condition. We recorded grizzle—the extent of light-colored pelage on the head and body—on a scale from 1–5 (Figure 4.2) and noted any changes in grizzle during subsequent field tracking. Genetic samples included whole blood preserved in ethylenediamine-tetraacetic acid (EDTA), flipper plugs (5x5-mm tissue samples taken from the hole created during application of flipper tags) preserved frozen or in 100% ethanol, plucked hair, and buccal swabs. Tissues were collected using standardized protocols (Tinker et al. *in review*) and stored at −20 to −80°C for subsequent DNA extraction and genetic analyses. We surgically implanted VHF radio-transmitters (Advanced Telemetry Systems Inc., Isanti, MN, USA) and applied color-coded plastic flipper tags (Temple Tags, Temple, TX, USA) using standard procedures (Williams and Siniff 1983, Monson et al. 2001).

Genetics: reproductive success and heterozygosity

We used tissue samples collected during capture and stranding events in Monterey, CA (N = 279) to isolate DNA and genetically type 37 microsatellite markers. These samples comprised 67 candidate fathers and 212 females, which included 205 candidate mothers and 183 candidate female pups (offspring/mother status was not mutually exclusive over the 14-study). Paternity analyses in CERVUS and FRANz identified father-pup pairs. Sample collection, DNA extraction, microsatellite markers, and paternity analyses are described in Chapter 3. All 37 microsatellite loci contributed to average heterozygosity for each male.

Space use: tracking and alternative space-use tactics

We tracked sea otters using VHF radio-telemetry and/or color-coded flipper tags every 3–5 days. Space-use analyses excluded males with fewer than 20 sighting locations in a two-year period to comply with minimum sample size requirements for home range estimation (Chapter 2). Home ranges were defined as the 90% probability contour within a two-year period using Permissible Home Range Estimation (Chapter 2). Landscape features were coastal position and distance from shore and the smoothing parameter was adapted as described in Chapter 2.

Home range characteristics comprised: (1) area; (2) length, defined as the distance along the 10-m isobath encompassed within the home range polygon(s); (3)

range span, or the total distance along the 10-m isobath from the northernmost to the southernmost points of the home range; (4) number of centers of use, where a center of use (COU) was a cluster of one or more polygons located >2 km from another polygon cluster within a home range; and (5) relative female density, which was approximated using the pup ratio (see *Study Location* section). Distinguishing male home ranges located within female- and male-dominated areas necessitated including relative female density. The metric does not approximate absolute female density, so it is not a direct substitute for access to estrous females.

The suite of home range characteristics was narrowed to those that were not significantly correlated ($R^2 > 0.7$). The scale function (R Development Core Team 2013) standardized the variance of the remaining home range characteristics and a k-means cluster analysis (Hartigan and Wong 1979) characterized space-use tactics. Analysis of similarities (ANOSIM) based on Bray-Curtis distances in the vegan package (Oksanen et al. 2015) tested whether assigned clusters were statistically distinct. A space-use transition matrix from year t to $t + 2$ defined the probability of using the same tactic or switching tactics in the next time step for males that were tracked for more than two years.

We explored the role of space use in mating probability by determining whether parent pairs identified through parentage analyses had greater home range overlap than randomly assigned female-male pairs. We calculated percent home range overlap for confirmed parent pairs, and then randomly matched the same females to our pool of all males and calculated female-male home range overlap. A

Wilcoxon Signed-Rank test (data were not normally distributed, Kolmogorov-Smirnov test, $p < 0.001$) tested whether parent pairs had higher home range overlap than random pairs.

Territory quality

Male territories are small, defended home ranges in female-dominated areas. Six territory features were hypothesized indicators of territory quality: (a) foraging opportunities, (b) kelp canopy availability, (c) shelter availability, (d) territory water depth, and (e) territory area. When male home range polygons extended beyond female-dominated areas, only resources within female-dominated areas were measured.

Cryptic prey items in rocky substrates, such as crabs, are rarely measured reliably by traditional subtidal SCUBA surveys but can comprise greater than 50% of sea otter diets (Tinker et al. 2008a). We thus extended the method of Garshelis et al. (1984)—who inferred the relative abundance of prey based on the presence of foraging females—by using existing data on diet and foraging success to determine the spatial distribution of key prey types and the potential energy return within male territories. We observed foraging otters (N = 81) around Monterey Peninsula and recorded prey species (e.g. abalone, clams, mussels) and prey size using methods previously described (Estes et al. 2003). Observations included foraging otters of every diet specialization type (Tinker et al. 2008a) to avoid biases in prey distribution due to individual diet preferences. The observations yielded average grams of each prey species consumed per minute for each forging bout, defined as multiple contiguous dives (N = 30–212 dives). Past studies calculated caloric values of each prey type using bomb calorimetry (Oftedal et al. 2007). A bootstrap model of foraging bouts (random draws of bouts with replacement) (Tinker 2004) calculated energy gain (kilocalories per minute) on a dive-by-dive basis by incorporating prey species, prey size, and observer biases (e.g. consumption of small prey is more likely to be underestimated).

Digitized aerial images collected in 1989, 1999, 2002–2006, and 2008 (Young 2014) yielded available GIS layers on persistent kelp (*Macrocystis pyrifera*) distribution in California (California Department of Fish and Game Marine Region 2014) (Figure 4.3), which were used to measure kelp canopy area within territories. During winter storm events females risk separation from their pups unless they find sheltered areas in which to rest and forage. An index of shelter and shoreline complexity—the length of coastline encompassed within a 500-m territory buffer divided by territory length—reflected shelter from wind and waves.

Proportional Hazards Model

A proportional hazards model (Sinha and Dey 1997) estimated the contributions of male attributes, space-use patterns, and territory resources to male siring success. In our analysis, siring success was a continuous process observed over discrete time intervals in an instantaneous hazards model. The likelihood of siring success (i.e. siring one pup) of an individual male over a particular time interval was given by the male's cumulative probability of possessing measured male characteristics, displaying certain space-use patterns, and acquiring territory resources over that interval. This analysis is most often employed to estimate the conditional probability of mortality, so the effects are termed "hazards" (Heisey and Patterson 2006). In this study, the instantaneous hazards at any point in time, *h*(*t*), were an approximation of the conditional probability of siring success over a short interval. In this way, the relative importance of particular covariates to siring success was estimated by hazards ratios (Heisey and Patterson 2006, Heisey et al. 2007, Halstead et al. 2012). We employed a non-parametric Kaplan-Meier approach (Sinha and Dey 1997) to estimate instantaneous proportional hazards from staggered-entry monitoring data, and then used these to estimate the contribution of fixed and random effects to siring success.

The log unit cumulative hazard (UCH or γ_r), which represented the additive effects of various log(hazards) within the time interval, and the probability of siring success, are given by equations 1 and 2 respectively,

$$\gamma_{r,i,j,g,m,h,t,a,d,v,f,l,b,u,n,e,c,k} = \gamma_0 + \rho_r + \delta_{i,j} + \beta_1 X_g + \beta_2 X_m + \beta_3 X_h + \beta_4 X_t + \beta_5 X_a + \beta_6 X_d + \beta_7 X_v + \beta_8 X_f + \beta_9 X_l + \beta_{10} X_b + \beta_{11} X_u + \beta_{12} X_n + \beta_{13} X_e + \beta_{14} X_c^2 + Z_k \qquad \text{Eq. 1}$$

$$S(s|r) = 1 - exp[-\textstyle\sum_{t=r+1}^{s} \exp(\gamma_t)] \qquad \text{Eq. 2}$$

where γ_0 represents the baseline log hazard rate, ρ_r represents the effect of time-varying hazards (proportion of pups sampled), $\delta_{i,j}$ represents the effect of age-varying hazards, β represents a vector of parameter values corresponding to the fixed-effects of covariates X (described below), and Z_k represents any additional random effects associated with individual *k* that were not accounted for by any of the fixed-effects in the model. *X* terms refer to the following fixed effects: grizzle (*g*), residual age-specific mass (*m*), heterozygosity (*h*), space-use tactic (*t*), territory area (*a*), territory depth (*d*), shelter index (*v*), territory prey availability (*f*), territory clam return (*l*), territory abalone return (*b*), territory mussel return (*u*), territory snail return (*n*), persistent kelp canopy area (*e*), and distance from the central capture location (*c*). Finally, γ_t in equation 2 represents the summation of log unit cumulative hazard values (from equation 1) over the period of interest and $S(s|r)$ represents the likelihood of siring from times *r* to *s*.

Bayesian Markov Chain Monte Carlo (MCMC) fitting algorithms in JAGS (Just Another Gibbs Sampler) (Plummer 2013) through the rjags package (Plummer 2015) fit both equations to our siring, attribute, space-use, and territory data. All parameters had uninformed priors. Model fitting included a burn-in period of 10,000 iterations, followed by 10,000 iterations across three chains. We graphically evaluated the traces from the three chains and examined $\hat{r}$ values to ensure model convergence and stability (Brooks et al. 2011).

Males entered the model at one year of age and their final interval ended in the year when they were last captured, sighted, or stranded. Males that did not sire a pup had one interval with a status of 1, indicating that no event occurred. Males that sired one or more pups had multiple non-overlapping intervals; intervals with no siring event had a status of 1, and intervals when a pup was sired had a status of 0. The minimum interval was 0.5 years so that each siring event was recorded in a separate interval (individual males in our study sired a maximum of two pups within a one-year period).

We assumed that male attributes (i.e. residual age-specific mass and grizzle) were informative for up to five years after they were measured, and patterns of space use (i.e. space-use tactic and territory resources) were informative for up to two years. All inputs were converted to residuals; 0 represented the average and unknown values were then assigned a value of 0. The term for each fixed effect was approximated by a normal distribution.

Male age was a continuously-varying effect estimated using non-parametric conditional auto-regressive (CAR) methods (Sinha and Dey 1997, Banerjee, S. et al. 2003). Individual identification was a random effect that accounted for non-independence of intervals. The proportion of pups sampled was a time-varying covariate that accounted for uneven sampling of pups across study years. Distance from our central capture location (the Monterey Bay Aquarium) was a random effect, as pup captures were more likely in that area. Random Bernoulli trails with probabilities from equation 2 represented siring success of each otter over each time interval. The MCMC algorithm maximized these binomial likelihoods (Heisey et al. 2007). Model comparisons (between the full model in equation 1 and simpler models with fewer effects) using DIC values (Spiegelhalter et al. 2002) determined which terms to include in the final model.

We report the effects of the covariates on the probability of siring success as the posterior distributions of log hazards ratios. The inclusion or exclusion of 0 within the 95% confidence intervals determined the significance of model parameters. A value of 0 corresponds to a hazard ratio of 1 (no significant effect), a value <0 corresponds to a ratio <1 or a reduction in hazard rates relative to baseline values, and a value >0 corresponds to a ratio >1 or an increase in hazard rates relative to baseline values. Other results are reported as mean ± standard deviation or median (quartile 1, quartile 3).

Results

Male space use

We tracked 72 tagged male sea otters—22 in Monterey, 7 in Big Sur, 7 in Piedras Blancas, 14 in Point Conception, 3 in San Luis Obispo, and 19 in Santa Barbara. Home range estimates used 127 ± 107 (range 20–539) locations per male of the 12,382 total sighting locations. Each home range encompassed two years of location data. We defined multiple temporally explicit home ranges for males with more than two years of location data, which lead to a total of 97 calculated home ranges (Table 4.1).

A cluster analysis of home range characteristics identified three space-use tactics (Figure 4.4). Dissimilarity between clusters was significantly greater than dissimilarity within clusters (ANOSIM statistic R = 0.8184, p = 0.001), so clusters were distinct. Home range area (PCA component 1 loading = −0.519) and pup ratio (PCA component 2 loading = −0.696) accounted for the greatest dissimilarity across clusters.

Cluster 1 home ranges (N = 54) were small (2.60 ± 2.41 km^2) in areas with a high proportion of females (0.18 ± 0.06 pups/independents). Field trackers recorded males using cluster 1 space-use tactics as territorial based on behavior for 82 (8, 97)% of their sighting locations, so we considered cluster 1 males to be territorial males. Cluster 2 and cluster 3 males were recorded as territorial for 39 (0, 80)% and 0 (0, 4)% of their sighting locations respectively. Cluster 2 home ranges (N = 32) were larger (11.54 ± 5.59 km^2) with a lower pup ratio (0.11 ± 0.05 pups/independents). Cluster 2 home ranges were located near the periphery of territorial male areas, so we henceforth refer to cluster 2 males as satellite males. Cluster 3 home ranges (N = 11) were the largest (28.40 ± 12.22 km^2) and were in areas of very low female density (0.05 ± 0.03 pups/independents) (Figure 4.5). Cluster 3 home ranges encompassed large areas of coastline, so we refer to cluster 3 males as transient males. Dissimilarity indices revealed that cluster 1 home ranges were most similar to each other; they clumped tightly in a principle components analysis and showed low within group variation. Cluster 3 home ranges had the highest within group variation and took up greater space in the principle components analysis.

We calculated transition probabilities between space-use tactics based on 25 males that we tracked for more than two years (Table 4.2). Territorial and satellite males were most likely to be territorial in the next two-year window (transition probabilities = 0.94 and 0.75 respectively). Satellite males were more likely to transition to a territorial tactic than were territorial males to transition to a satellite tactic (transition probability = 0.06). There was only one instance out of 17 possible cases where a male transitioned from a territorial to a satellite tactic in the next time step. We did not track any of the 11 transient males for greater than two years, so it is unknown whether these males are more likely to remain transient or transition to one of the other space-use tactics in subsequent years. These transition probabilities indicate an inherent age effect in the use of space-use tactics, where satellite males transition towards territoriality with age.

Predictors of reproductive success

Paternity analyses in CERVUS identified 23 father-pup pairs with strict criteria (95% confidence) and 40 with relaxed criteria (80% confidence) (Chapter 3). Most males (81% with strict criteria or 61% with relaxed criteria) received zero paternity assignments across the 14-year study, and the most successful males acquired three paternities. Detailed results for paternity analyses are presented in Chapter 3. We ran the proportional hazards model with both strict and relaxed paternity assignments. Parameter estimates did not differ significantly so we employed relaxed paternity assignments in the final model for greater statistical power.

The full model had high predictive error (DIC = 313, pD = 63), and there was no random effect of individual (Z_k) (parameter estimates included 0 within the 95% confidence intervals for each individual), so we excluded the individual term. The full model without the random effect of individual had lower predictive error (DIC = 283, pD = 19) compared to a model with only male attributes (DIC = 288, pD = 12). Including both male attributes (Table 4.3) and territory resources (Table 4.4) therefore resulted in a better model fit.

Among male attributes, siring success was best predicted by male age (Table 4.5). The predicted probability of siring steadily increased from low values at age three (0.01) until it peaked at ages six (0.13) and seven (0.13), followed by a steady decline back to low predicted probabilities of siring (0.03) by age eleven (Figure 4.6). Note that siring probabilities reflect relative estimates, so should be compared to each other without direct interpretation of the values. While included in the best-fit model, mass, grizzle, and heterozygosity had little effect on the predicted probability of siring (Figure 4.7).

Eighteen of the 67 males that were sampled for paternity analyses had corresponding location data, comprising 13 territorial, four satellite, and one transient male. Territorial males gained 20 paternities, satellite males gained 2 paternities, and transient males gained 0 paternities (16 males with unknown space use were assigned the remaining 18 pups). The effect of male space-use tactic (cluster term) had a parameter estimate that included 0 within the 95% confidence intervals, indicating no notable deviation from a log hazards ratio of 1.

The parameter estimate for kelp canopy was strongly positive (Table 4.5), indicating that males with more kelp canopy in their territories have a higher predicted probability of siring. Territory resources were included in the best-fit model, but other territory resources influenced siring success to a lesser extent. As expected, males were more likely to be assigned a pup through paternity analyses if they were closer to the central capture location. There was also a positive effect of the proportion of pups sampled in a given year on the probability of siring.

Parents—female-male pairs that were assigned the same offspring through parentage analysis—tended to have high home range overlap (Figure 4.8). A comparison between home range overlap of parent pairs and randomly assigned female-male pairs revealed that parents had significantly more home range overlap ($V = 1564$, $df = 59$, $p << 0.0001$) (Figure 4.9).

Discussion

We characterized the southern sea otter mating system by quantifying male reproductive success and identifying the physical and behavioral characteristics that influence the probability of male siring success. We expected that older, larger males would have higher reproductive success. Reproductive success was predicted by age, but there was little indication that grizzle or body mass influenced reproductive success. We expected that the most successful males would hold reproductive territories containing abundant resources, such as prey, kelp, and shelter. Both territorial and non-territorial males gained paternities, and space-use tactic did not affect the probability of siring in the final model. Among territorial males, siring was more likely when males defended territories containing a large area of kelp canopy, but other resources such as prey and shelter had no notable effect on siring success (Table 4.5). This is the most extensive study of male reproductive success in sea otters; our sample size for territorial males exceeds all previous studies (2–12 territorial males) (Pearson et al. 2006), as does our sample of satellite and transient males whose reproductive success has never been quantified.

Male Attributes

The effect of male age on siring success agrees with previous estimates that sexual maturation in male southern sea otters occurs during the fifth year of age, and that sexual potency continues past age twelve (Green 1978). The males in this study achieved peak siring probabilities just after the age of first reproduction at ages six and seven years. After this peak, siring probability steadily declined with age, although it remained elevated above 0 through age eleven. There was also a small peak in error around siring probability estimates at age 14 because we found two males that sired pups at the maximum age of 14. Five males in our study sired at age five, while Alaskan sea otters were not observed copulating before age six (Garshelis et al. 1984). This difference could be accounted for by uncertainty in age estimates, which are based on expert opinion and tooth wear and can be confounded by diet, or southern sea otters may reproduce earlier than northern sea otters. Age-specific siring probabilities (Figure 4.6) reflect the probability of siring given that a male has survived to that age. Since declines in siring probabilities are independent from survivorship, the decline in siring probability after age seven suggests reproductive senescence in this species. The low siring probabilities of males over the age of eleven aligns with a steady decrease in male annual survival rate from ages eleven to sixteen (Tinker *et al. in review*), and suggests that selective pressure on male reproductive ability may be weak at older ages, resulting in reproductive senescence.

Previous work on the Alaskan sea otter (*Enhydra lutris kenyonii*) mating system showed that male size influenced the number of copulations obtained by males (Garshelis et al. 1984). In contrast, our results indicate no effect of residual age-specific mass on siring success. Mass increases with age in male sea otters, so previous studies of northern sea otters may have identified an effect of both age and mass because the two are correlated. We corrected for age by calculating the residual mass from a fitted mass-by-age curve. Our analysis suggests that mass does not influence siring success independent of the age effect.

Similar to mass, grizzle and heterozygosity did not affect the probability of siring. The mean parameter estimate was slightly positive for grizzle, but overall did not deviate from zero. Some successful males seemed to have higher levels of grizzle, however grizzle tends to increase with age, and the effect of grizzle did not emerge with age accounted for in the model. These results suggest that grizzle may act as a cue to communicate age or experience, as previously suggested (Garshelis et al. 1984), but is not a cue for quality independent of age.

Male Space Use

We identified three distinct patterns of space use and tracked males for up to eight consecutive years as they transitioned between tactics. There existed an inherent age effect of space-use tactics, where males transitioned from a satellite tactic with home ranges of intermediate area to a territorial tactic with very small home ranges in female-dominated areas. We were unable to track transient males for multiple years, so the ontogeny of that space-use tactic remains unknown.

Male space-use tactic did not affect the probability of siring in the hazards model. Undetected effects of some predictors on siring success, notably space-use tactic, may be directly related to insufficient power in our analysis. In particular, we had little power to detect the effect of space-use tactic due to biased sampling of males and their pups. Weather conditions and travel time restricted genetic sampling in areas distant from the boat launch site (proximate to the Monterey Bay Aquarium). The central capture location is within a female-dominated area, so we were more likely to sample territorial males than satellite or transient males. As a consequence of biased sampling, space use was known for 13 territorial, four satellite, and one transient male out of 67 males total. Furthermore, we were more likely to sample the pups of territorial males than the pups of satellite or transient males. The parameter estimate for distance from the central capture location, ß(14) (Table 4.5), deviated from zero, signifying a negative effect of distance on siring probability. Siring success of males at the edges of the study area was therefore underestimated. Transient males can swim the length of the southern sea otter range, so likely sire pups far beyond the central capture location and our study site.

In addition to more even sampling in space, additional sampling of pups would improve model power. The parameter estimate for the proportion of pups sampled in each year indicated a positive effect of sampling on siring probability. Additional sampling of pups would uncover more siring events, and allow for greater power to detect parameters that affect siring probability.

The high degree of home range overlap between parent pairs (Figure 4.9) suggests that male space use plays a key role in reproduction, so it would not be surprising if space-use tactic emerged as an important indicator of siring success with additional sampling. Notably, both territorial and satellite males sired pups. The reproductive payoff of these alternative space-use tactics remains to be determined. Additional sampling and analyses would reveal whether these tactics constitute alternative mating tactics or if the transient and satellite tactics simply represent age-specific transition phases on the way to territoriality.

Territory Quality

Early work on the mating system of northern sea otters found that territory quality affected copulations (Garshelis et al. 1984). High quality territories were large, enclosed, accessible (the entrance was not adjacent to another territory), and contained prey. In contrast, we found that the probability of siring was not influenced by territory area, shelter, or prey return in southern sea otters, but that kelp canopy had a strong positive effect on siring probability.

Kelp canopy offers females and pups protection from waves during winter storm events in California. If we consider kelp canopy to be a form of shelter from waves and prevailing winds, then there are similarities in the results for northern and southern sea otters. Although our index of shelter based on coastline complexity did not influence siring probability, shelter offered by the coastline is much less variable in California compared to Alaska. The study site in Alaska comprises many small coves and inlets that are physically protected, whereas the Monterey, CA coast is much less complex and exposure varies little. Kelp canopy thus may be a better indicator of shelter than coastline complexity in California, whereas shelter in Alaska is sufficiently offered by physical protection. Results from both studies suggest that shelter and protected resting areas for mothers and pups is an important resource that impacts male reproductive success.

This study provides the first documented evidence that kelp influences sea otter reproduction. The positive effect of sea otters on kelp abundance—which comes about through a trophic cascade where sea otters reduce sea urchins and release kelp from predation—is well documented in rocky nearshore habitats (Estes and Palmisano 1974). Kelp has positive effects on sea otters; kelp provides resting areas and habitat for sea otter prey. Our results show a large positive effect of kelp availability on male reproductive success. Taken together, current evidence suggests that sea otters alter the environmental potential for polygyny, and that males effectively create their own opportunities for mating. There seems to be significant feedback between behavior and ecology. This raises the question of the degree to which other species can influence the environmental potential for polygyny through behavior.

This study does not agree with the conclusion that defending prey patches increases male reproductive success. Our conclusions may differ from those of the northern sea otter study because we used different methods to estimate reproductive success. Garshelis et al. (1984) used observed copulations to quantify reproductive success; this study used paternity analysis. Copulations and consort behavior do not necessarily equal siring success (Pemberton et al. 1992, Hughes 1998, Coltman et al. 1999).

Putting the methodological discrepancies aside, there may be true differences in the importance of prey to territory quality in northern and southern sea otters due to differences in resource distribution. Resources are limited in Monterey, CA and the population is at or near carrying capacity (Tinker et al. 2008a). There was low variability in prey return across territories, suggesting that prey resources are evenly distributed. If resources are more abundant and distributed in patches in Alaska, then females may aggregate around profitable foraging patches and males may have a greater opportunity to monopolize females by defending prey resources (Emlen and Oring 1977).

This study supports the role of resource defense in the sea otter mating system. The importance of shelter in studies of both northern and southern sea otters begs the question of whether shelter is always an important resource. Sea otters inhabit not only exposed coastlines, but also sheltered estuaries, such as Elkhorn Slough in California. Home ranges estimated using VHF radio-telemetry in Elkhorn Slough show that males still use the territorial tactic in this sheltered habitat. Future work could explore which resources become important to male reproductive success when exposure to storm events is a minimal threat to females.

Conclusion

This study characterized the sea otter mating system by determining the male physical and behavioral characteristics that influence reproductive success. Siring probability becomes elevated at age five, peaks at age seven, and remains elevated until age eleven. Males reproduced until at least 14 years of age. Male sea otters employ alternative space-use tactics, and at least two of the three tactics confer siring success. The exact reproductive payoffs of these tactics remain to be determined, offering an avenue for future work on this mating system. Territorial males experience a higher probability of siring when they defend more kelp canopy. In contrast to studies of the Alaskan subspecies, prey was not important to territory quality, and may be related to less variable prey availability in California.

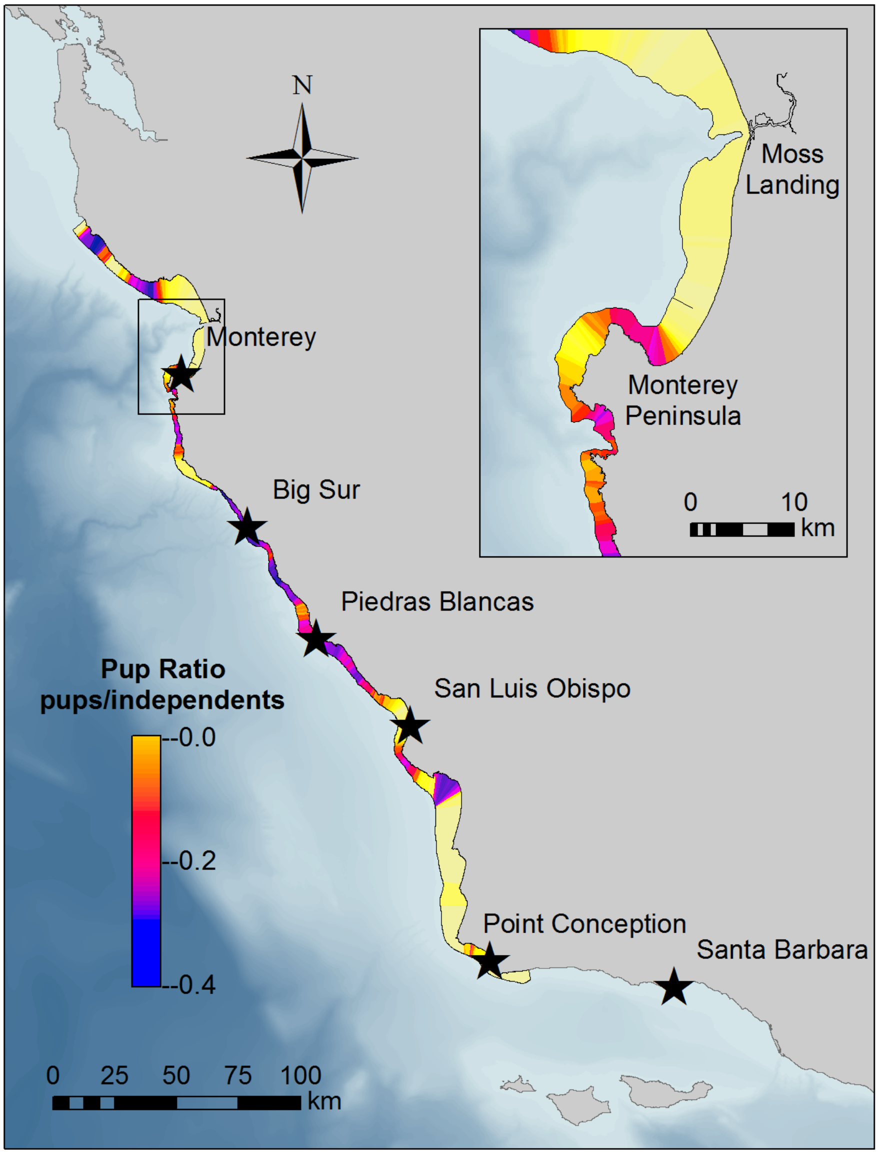

Figure 4.1. Extent of male- and female-dominated areas throughout the southern sea otter range in California. The pup ratio (pups/independents) was calculated using survey census data (spring 2003 is depicted here). Male-dominated areas exist where the pup ratio is < 0.1 (yellow). Female-dominated areas have a pup ratio > 0.1. Stars indicate capture locations for space-use data. The primary study area for genetics, Monterey Peninsula, is enlarged in the inset.

Figure 4.2. Photos of sea otters with different levels of grizzle—the extent of light-colored pelage on the head and body. Pictured from left to right are animals with none to slight grizzle (level 1), with grizzle from the nose to the eyes (level 2), to the lambdoidal crest (level 3), to the chest (level 4), and to the tail (level 5). Photo credits: B. Lyon (1,3) and J. Tomoleoni (2,4,5).

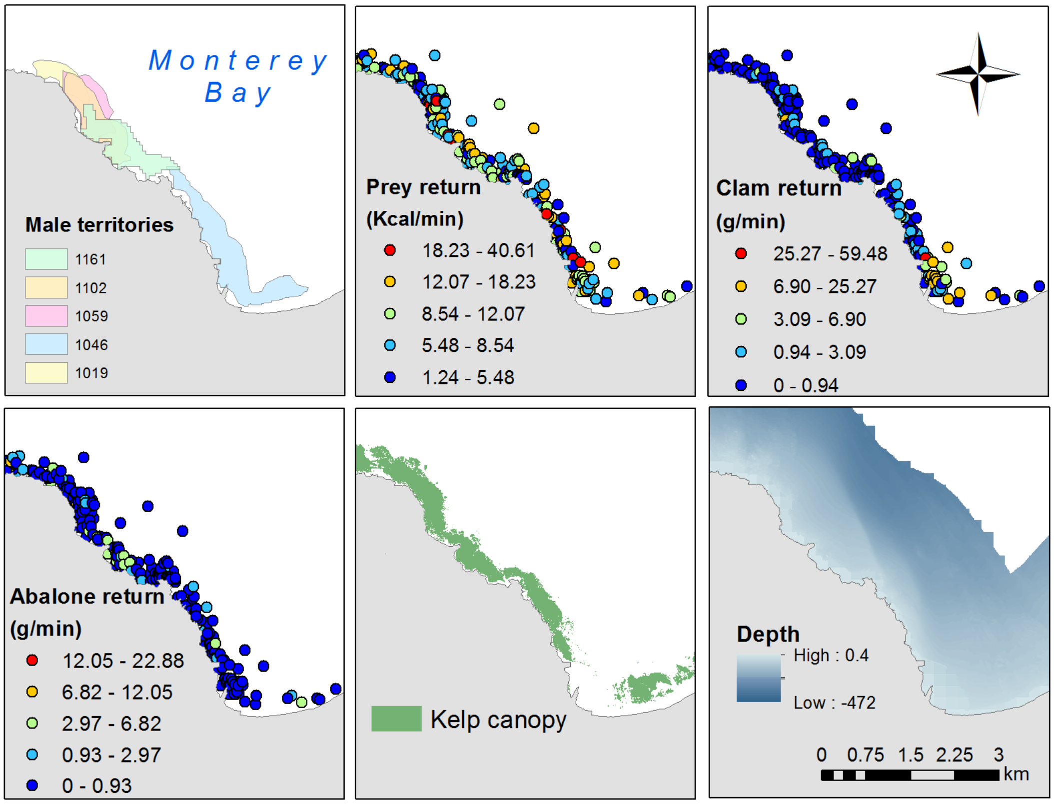

Figure 4.3. Male sea otter territories with resources in Monterey, CA. Select territories present in 2003 are depicted. Resource layers include: prey return (top center), clam return (top right), abalone return (bottom left), kelp (bottom center), and depth (bottom right). Prey availability was estimated based on observed sea otter foraging bouts in the area (each point represents a bout composed of multiple dives). During each foraging bout, observers recorded prey species and size. Maps are projected in CA Teale Albers NAD 1927.

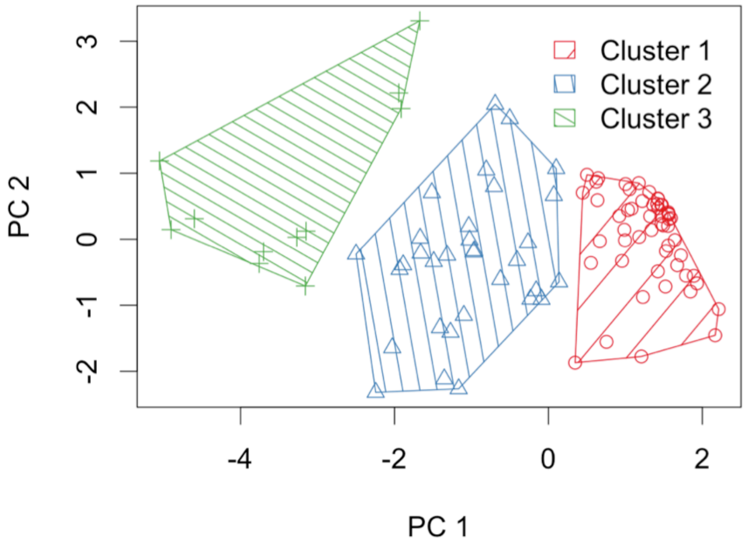

Figure 4.4. Male space-use tactics along two principle components of home range characteristics. Males were grouped based on five characteristics: mean pup ratio, sd pup ratio, home range area, range span, and number of centers of use. PC1 falls along increasing pup ratio and decreasing metrics of home range size. PC2 indicates decreasing pup ratio and centers of use, and increasing range span. We used the raw data for home range characteristics in the k-means cluster analysis; PCA is used here for visualization only.

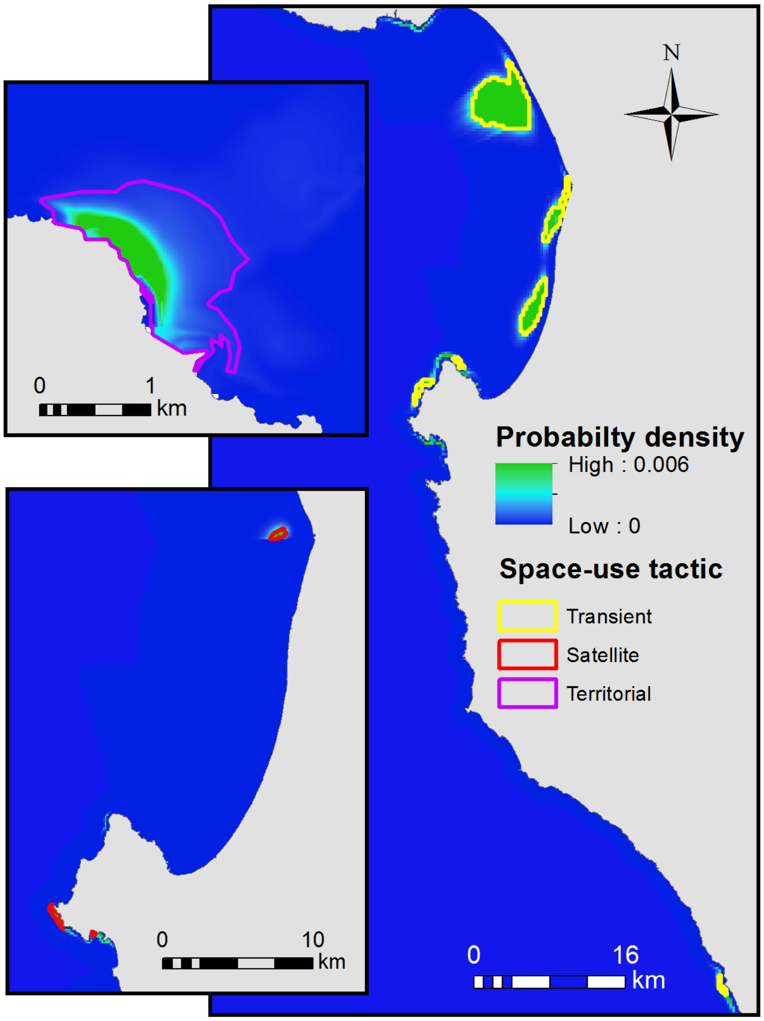

Figure 4.5. Map showing representative home ranges for males of each space-use tactic. Territorial males had small home ranges in female-dominated areas (purple). Satellite males had medium-sized home ranges in both female- and male-dominated areas (red). Transient males traveled extensively, had large home ranges, and were primarily located in male-dominated areas (yellow). Scaled colors show the probability density from Permissible Home Range Estimation and outlines depict the 90% probability contour. Note the discrepancy in the scale bars for each home range.

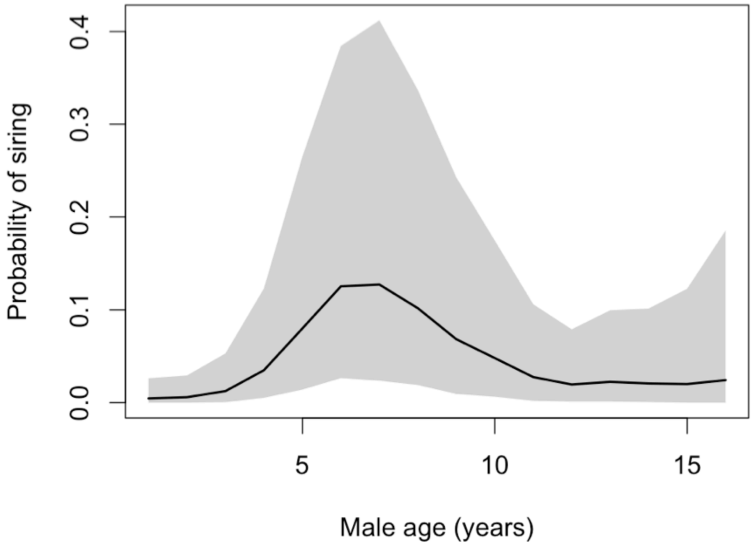

Figure 4.6. Relative predicted probability of siring as a function of male age from the proportional hazards model. The black line shows the non-parametric conditional auto-regressive model and the gray shading represents 95% confidence intervals.

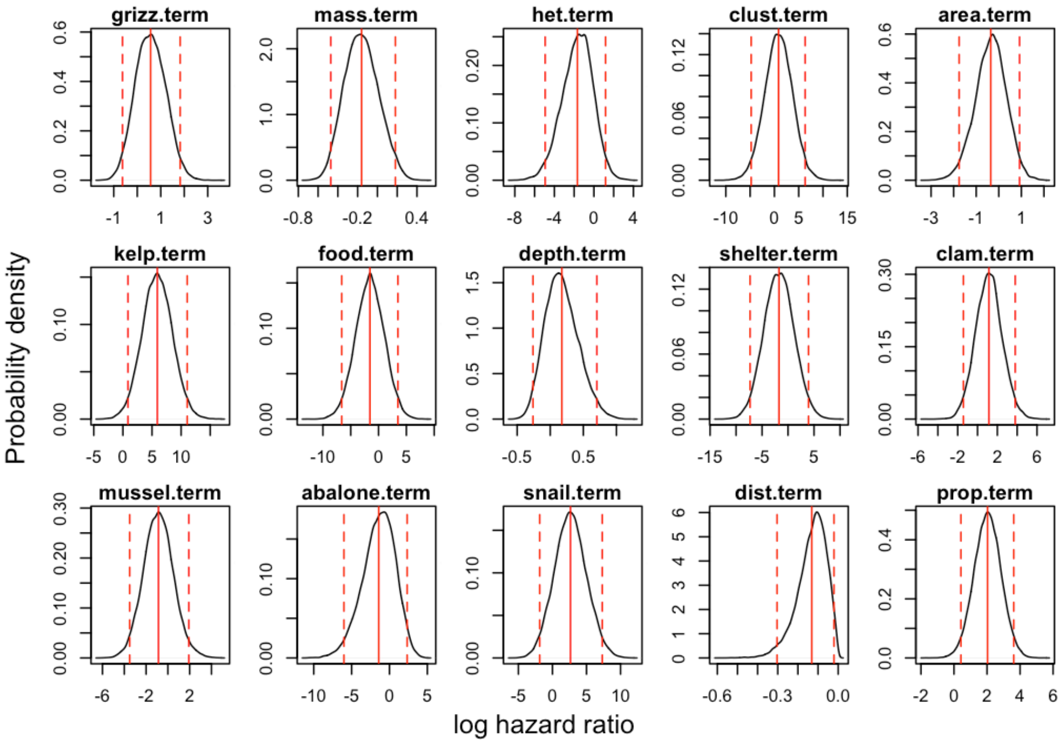

Figure 4.7. Bayesian posterior distributions for model estimates of fixed and random effects. The mean value is indicated by the solid line and the dashed lines indicate upper and lower 95% confidence intervals. Parameters with posterior distributions that exclude 0 from between the 95% confidence intervals are interpreted as having an effect on siring success, where mean values below 0 indicate a negative effect on siring success and mean values above 0 indicate a positive effect on siring success. From left to right, parameter estimates are shown for grizzle, mass, heterozygosity, space-use tactic (cluster), and territory area (row 1); territory kelp area, prey return, depth, shelter index, and clam return (row 2); mussel return, abalone return, snail return, distance from the central capture location, and the proportion of pups sampled by year (row 3). Not shown are posterior distributions of rho (age parameter). Summary statistics for all parameters are in Table 4.5.

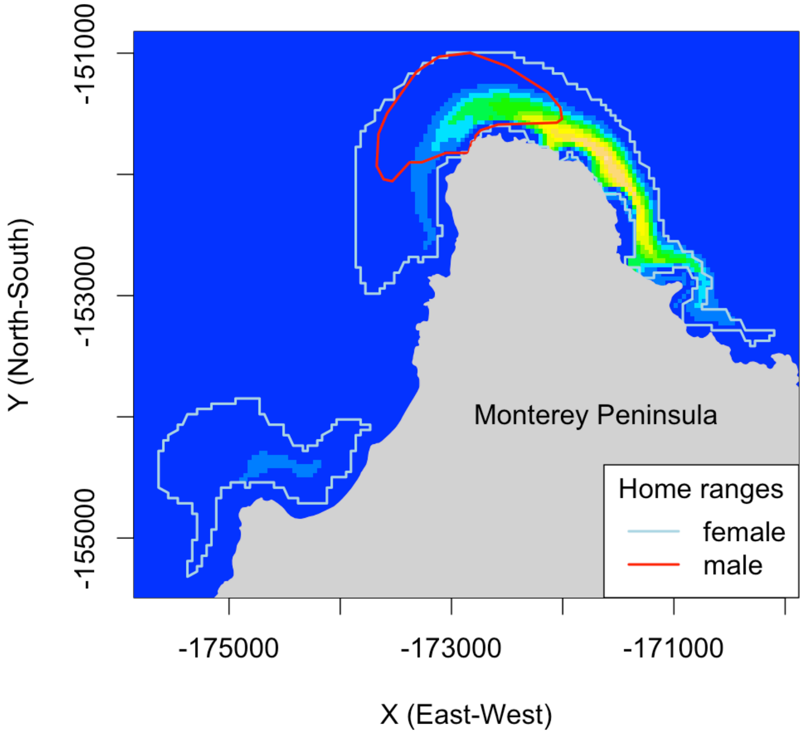

Figure 4.8. Map of home range overlap of a parent pair. Male 1235/5408 (blue) and female 1214/5478 (red) produced two pups together in 2005 and 2006. The probability density surface for 1214 is depicted with the 90% probability contour for 1235/5408 (blue) and 1214/5478 (red). The map projection is California Teale-Albers NAD 1927 and the coordinates are in meters.

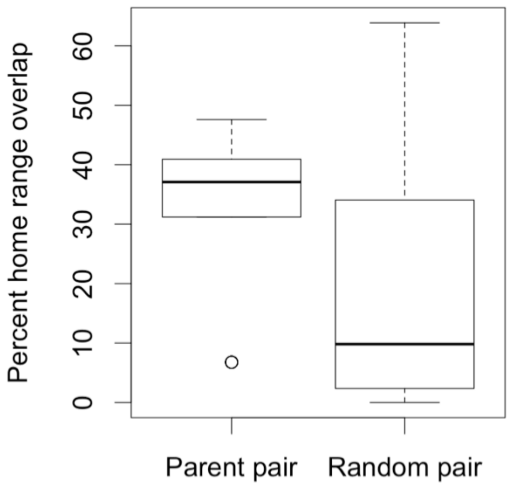

Figure 4.9. Home range overlap for parent pairs versus random pairs. Home ranges of parent pairs overlapped significantly more than home ranges of randomly selected female-male pairs.

Table 4.1. Summary statistics of home range characteristics for males by cluster. Length is the distance along the 10m bathymetric contour within the home range polygon(s). Range span is the length along the 10m bathymetric contour from the northernmost to the southernmost points of the home range. Centers of use (COU) are defined as a cluster of one or more polygons within a home range that is at least 2 km from another polygon cluster. Values are reported as median (quartile 1, quartile 3).

Home range characteristic	Cluster 1	Cluster 2	Cluster 3	All males
N	54	32	11	97
Area (km^2)	1.60 (0.77, 3.61)	10.31 (7.85, 13.36)	28.03 (17.85, 39.09)	5.98 (1.33, 11.87)
Length (km)	3.51 (2.26, 5.20)	13.48 (10.02, 15.78)	31.97 (15.30, 35.91)	6.91 (3.44, 13.75)
Range span (km)	3.70 (2.12, 7.86)	51.41 (22.55, 136.00)	209.20 (183.10, 276.30)	15.10 (3.42, 109.80)
Number of COU	1 (1, 1)	2.5 (1, 3)	5 (3, 5)	1 (1, 3)
Pup ratio	0.16 (0.14, 0.22)	0.11 (0.07, 0.15)	0.06 (0.04, 0.07)	0.14 (0.09, 0.17)
Pup ratio sd	0.01 (0.01, 0.02)	0.07 (0.05, 0.07)	0.05 (0.04, 0.07)	0.02 (0.01, 0.06)

Table 4.2. Transition probabilities between male space-use tactics. Individuals start as the cluster indicated by the columns and transition to the cluster indicated by the rows in the subsequent two-year time window.

	Tactic at time *t*		
Tactic at time *t* + 2	Territorial (cluster 1)	Satellite (cluster 2)	Transient (cluster 3)
Territorial (cluster 1)	0.94	0.75	No data
Satellite (cluster 2)	0.06	0.25	No data
Transient (cluster 3)	0.00	0.00	No data

Table 4.3. Summary statistics for male attributes. N is the number of males for which the attribute information was available from capture and stranding records.

Attribute	N	Median	Quartile 1	Quartile 3
Birth year	67	1996	1994	1999
Grizzle	50	3	2	4
Mass (kg)	52	27.50	24.08	30.55
Age-specific mass deviation	52	−2.43	−4.55	0.62
Heterozygosity	67	0.46	0.41	0.51

Table 4.4. Summary statistics for territory resources (N = 18). Prey return represents the mean value for the territory.

Resource	Median	Quartile 1	Quartile 3
Depth (m)	−12.88	−21.56	−7.82
Shelter index	1.33	1.17	1.44
Prey return (kcal/min)	9.27	8.79	9.43
Clam return (g/min)	0.49	0.30	1.88
Abalone return (g/min)	0.62	0.15	1.36
Mussel return (g/min)	0.78	0.26	1.71
Snail return (g/min)	0.30	0.13	1.02
Persistent kelp canopy (km^2)	0.47	0.36	0.64

Table 4.5. Bayesian model parameter estimates for log(hazard) function (Equation 1). All parameters represent log(hazard) ratios. Parameters that deviate from 0 are indicated with *.

Param.	Description	Mean	sd	L 95% CI	H 95% CI	f
$\beta(1)$	Grizzle effect	0.57	0.64	−0.63	1.83	0.81
$\beta(2)$	Mass effect	−0.16	0.17	−0.47	0.18	0.82
$\beta(3)$	Heterozygosity effect	−1.67	1.56	−4.93	1.18	0.86
$\beta(4)$	Space-use tactic effect	0.85	2.84	−4.79	6.33	0.62
$\beta(5)$	Home range area effect	−0.36	0.68	−1.76	0.92	0.70
$\beta(6)$	Home range depth effect	0.18	0.25	−0.26	0.70	0.75
$\beta(7)$	Home range shelter index effect	−1.74	2.88	−7.30	3.95	0.73
$\beta(8)$	Mean prey (kcal/min) effect	−1.55	2.57	−6.62	3.48	0.73
$\beta(9)$	Clam (g/min) effect	1.15	1.33	−1.43	3.80	0.81
$\beta(10)$	Abalone (g/min) effect	−1.42	2.15	−6.01	2.33	0.73
$\beta(11)$	Mussel (g/min) effect	−0.86	1.37	−3.50	1.92	0.74
$\beta(12)$	Snail (g/min) effect	2.65	2.34	−1.87	7.32	0.87
$\beta(13)$*	Kelp effect	5.91	2.59	0.87	11.05	0.99
$\beta(14)$*	Distance from center effect	−0.13	0.07	−0.30	−0.02	1.00
ρ*	Proportion of pups sampled effect	2.03	0.81	0.42	3.62	0.99
$\delta(1)$*	Age-specific hazards, age 1	−6.57	2.02	−11.58	−3.63	1.00
$\delta(2)$*	Age-specific hazards, age 2	−5.99	1.61	−9.93	−3.52	1.00
$\delta(3)$*	Age-specific hazards, age 3	−4.91	1.14	−7.46	−2.91	1.00
$\delta(4)$*	Age-specific hazards, age 4	−3.65	0.82	−5.23	−2.03	1.00
$\delta(5)$*	Age-specific hazards, age 5	−2.77	0.79	−4.25	−1.18	1.00
$\delta(6)$*	Age-specific hazards, age 6	−2.25	0.75	−3.62	−0.72	1.00
$\delta(7)$*	Age-specific hazards, age 7	−2.25	0.79	−3.73	−0.63	1.00
$\delta(8)$*	Age-specific hazards, age 8	−2.50	0.78	−3.95	−0.89	1.00
$\delta(9)$*	Age-specific hazards, age 9	−2.98	0.85	−4.65	−1.28	1.00
$\delta(10)$*	Age-specific hazards, age 10	−3.36	0.86	−5.04	−1.65	1.00
$\delta(11)$*	Age-specific hazards, age 11	−4.03	1.01	−6.17	−2.19	1.00
$\delta(12)$*	Age-specific hazards, age 12	−4.42	1.08	−6.73	−2.50	1.00
$\delta(13)$*	Age-specific hazards, age 13	−4.39	1.14	−6.73	−2.26	1.00
$\delta(14)$*	Age-specific hazards, age 14	−4.61	1.32	−7.36	−2.24	1.00
$\delta(15)$*	Age-specific hazards, age 15	−5.12	1.83	−9.16	−2.03	1.00
$\delta(16)$*	Age-specific hazards, age 16	−5.73	2.70	−11.93	−1.58	1.00

Chapter 5

Conclusion

Animal movement and space use determine the physical and biotic environments with which an individual interacts, and have implications for habitat selection and mating systems. I analyzed space use of a marine predator, the sea otter, to characterize the mating system and identify the impacts of movement behavior on reproductive success. This dissertation outlined a novel method of defining space use, provided the first confirmed estimates of siring age in male sea otters, afforded evidence for important feedbacks between behavior and ecology in mating systems, and paved the way for future investigations of exposure to pollutants and range expansion of a threatened species.

Home Range Estimation

A home range is the area to which an animal restricts its movement and performs regular activities such as foraging, resting, and mating (Burt 1943). Previous statistical methods of estimating home ranges were inadequate for coastal marine species because they were unable to correctly account for the complexity of coastal habitat, and incorrectly encompassed areas of land (an unused habitat type) in home ranges. This research provided a novel algorithm in spatial statistics for estimating animal space use in restricted habitats. The method enables the user to incorporate information about the environment into home range estimates to allow for greater accuracy in home range shape and exclusion of unused areas. This new approach will improve understanding of habitat requirements and conservation efforts in multiple species.

The Long-Game Approach of Sea Otter Reproduction

This study provided the first opportunity to explore when and how male sea otters reproduce based on genetic paternity assignments. We found that males do not reproduce until age five, although they become physiologically capable of reproducing within the preceding year (Green 1978). Anatomical estimates suggest that sexual potency can continue past 12 years of age (Green 1978). My results confirm this prolonged ability to sire, and show that males of up to 14 years of age sire pups. Males maintain an extended reproductive lifespan; siring probability is elevated through age 11 and some males maintain reproductive territories for eight consecutive years. This evidence points to a long-game approach to reproductive success, where males invest in survival and gain paternities over time.

Feedbacks between Behavior and Ecology

This research supports a mating system characterized by resource defense, where males defend large patches of kelp that offer shelter to females and their pups. This constitutes the first documented evidence that kelp has a positive effect on sea otter reproductive success. The trophic cascade by which sea otters enhance the abundance of kelp in rocky nearshore ecosystems has been well documented (Estes et al. 1978). This study offers evidence that abundant kelp, in turn, supports successful reproduction of male sea otters. There may exist a positive feedback loop upon establishment of sea otters, where sea otters prey on benthic invertebrates and release kelp from predation pressure, and the subsequent increase in kelp provides suitable resting/mating habitat and attracts more sea otters. In this way, the presence of otters increases the environmental potential for polygyny, and males effectively create their own opportunities for mating. The degree to which animals can influence the environmental potential for polygyny through their behavior merits further investigation.

Future Directions

Patterns of animal space use affect not only mating systems, but also access to resources and exposure to risks. Male sea otters exhibit three distinct patterns of space use that differ greatly in their movement distances and home range area. These differences are relevant for sea otter health and conservation, as nearshore habitats receive terrestrial pollutants through runoff, and previous work on sea otters found that habitat use influences exposure to terrestrial pathogens (Johnson et al. 2009). Territorial males are expected to be subject to local threats and limited by local resources, whereas transient males are subject to a greater diversity of threats because their home ranges encompass multiple watersheds. Future work could synthesize the reproductive and energetic payoffs of each space-use tactic, as well as the costs in terms of exposure to sources of mortality.

An understanding of male space-use tactics will enhance efforts to predict range expansion in this threatened species. Sea otter populations at the center of the range are at or near carrying capacity and are resource-limited (Tinker et al. 2008a). Population growth therefore requires dispersal outside of the current range. Males initiate expansion and facilitate female establishment (Lafferty and Tinker 2014). Transient males make more likely colonizers because of their long-range movement behaviors, but their transition to territoriality may be important for female establishment. Future work should explore the space-use tactic of colonizers and how the ontogeny of space-use tactics facilitates or slows range expansion.

Appendix

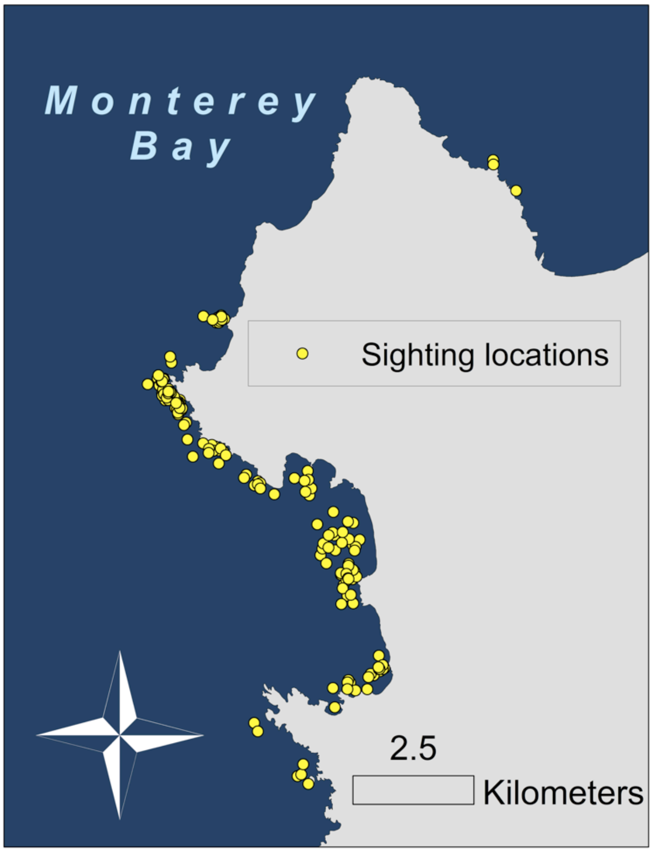

Figure A1. Step 1 of Permissible Home Range Estimation: Sighting locations of an individual animal are collected over a set time period. Sighting locations of sea otter 1317, a female in Monterey Bay, CA, over a two-year period (2007–2009). Data were collected using VHF radio-telemetry. Projection: CA Teale Albers, NAD 1927.

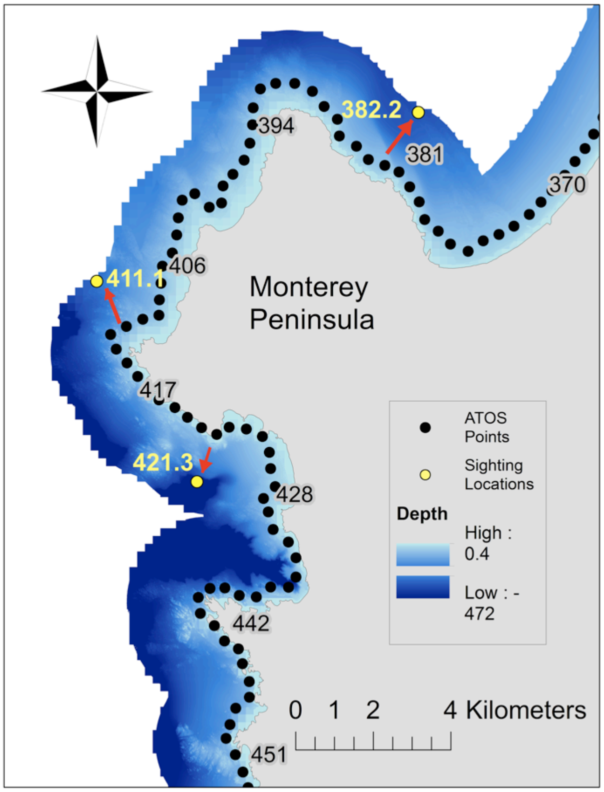

Figure A2. Step 2 of Permissible Home Range Estimation: Sighting locations are transformed from geographic coordinate space to landscape space. For sea otters, we assigned coastal position (ATOS) and distance from shore values to sighting locations. ATOS (As The Otter Swims) points are numbered sequentially and run along the 10-m isopleth at 500-m intervals (black points and numbers). Sighting locations (yellow points) are each assigned an ATOS value (yellow numbers) based on their proximity to ATOS points and a distance-from-shore value based on their distance to the closest point on land (vector along the red arrows).

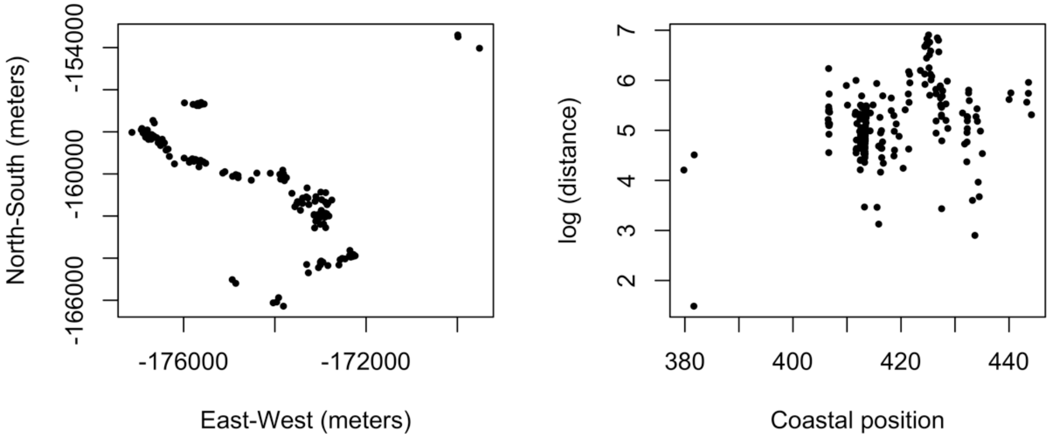

Figure A3. Step 2 continued: Sighting locations are transformed from geographic coordinate space (left) to landscape space (right).

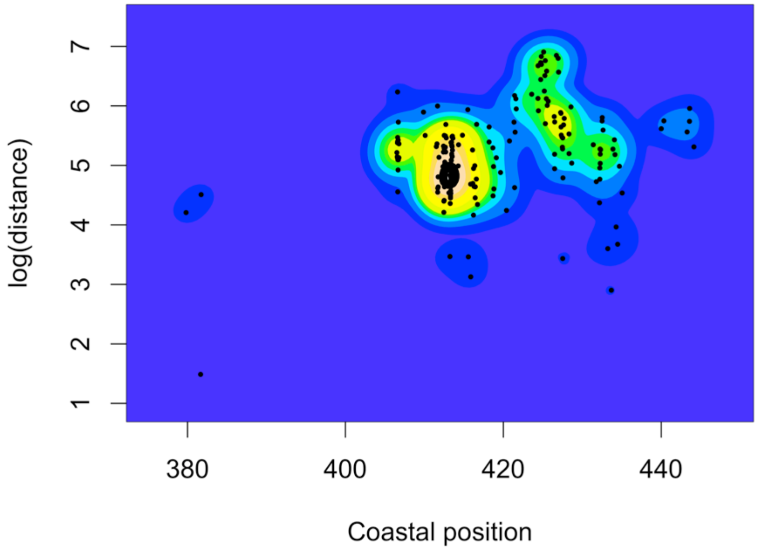

Figure A4. Step 3 of Permissible Home Range Estimation: A kernel density function is generated in landscape space. Black points denote ATOS and *log*(distance) values of the sighting locations. Warmer colors indicate increasing density values.

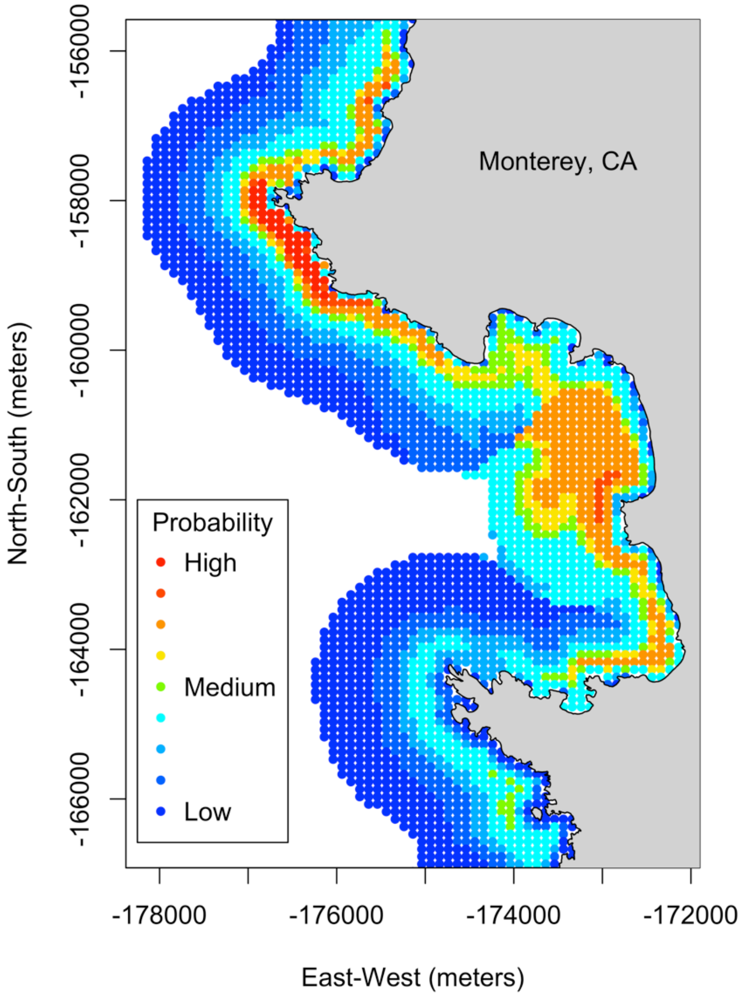

Figure A5. Step 4 of Permissible Home Range Estimation: Kernel density estimates are back-transformed to geographic coordinate space and converted to probability estimates. Using the kernel density function, density values are calculated for each point in a regularly spaced array along the central California coast. All kernel density values in the array are transformed to sum to one and reflect probability values. Projection: CA Teale Albers, NAD 1927.

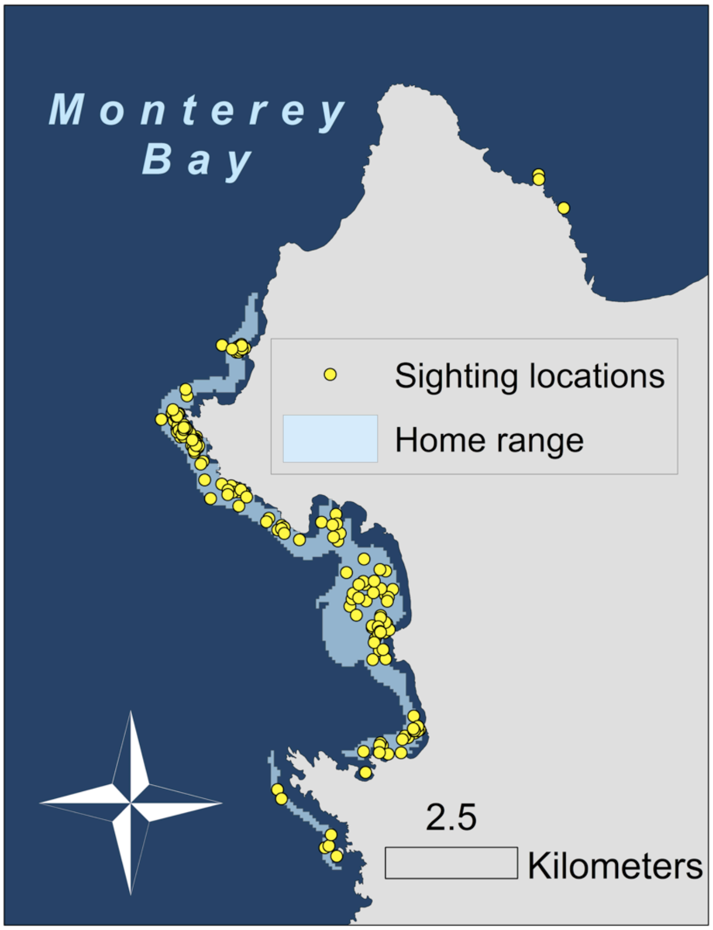

Figure A6. Step 5 of Permissible Home Range Estimation: Array points within the 90% probability kernel are selected and converted to a polygon, which defines the boundaries of the permissible home range. Grid points with probability values within the 90% probability kernel are selected and converted to a polygon to define a permissible home range. Projection: CA Teale Albers, NAD 1927.

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