Territory quality of male sea otters in Prince William Sound, Alaska: relation to body and territory maintenance behaviors

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Abstract: Based on optimality models, lekking males holding higher quality territories should spend more effort on territory maintenance and less effort on body maintenance. We tested the hypothesis that benefits are correlated with costs for male sea otters, *Enhydra lutris* (L., 1758). Activity state was recorded during focal follows of 10 individuals (n = 127). Higher quality territories had larger area, more food resources attractive to females, a higher ratio of protective shoreline edge, and higher accessibility for females evading male harassment. Contrary to our prediction, territory quality was uncorrelated with measures of cost: territory maintenance (patrolling, interacting) and body maintenance (feeding, grooming). We rejected the hypothesis that proximate benefits would be correlated with costs and suggested the following alternative working hypotheses: (*i*) given the high metabolic rate of sea otters, male breeding success may depend as much on maintaining body condition as maintaining a territory; (*ii*) higher quality territories with shoreline edge may not require additional patrolling effort; (*iii*) males may not expend extra effort in territory maintenance until more females come into estrus; or (*iv*) our seasonal measures of the benefits and costs of territoriality may not have accurately reflected factors influencing the switch between territorial and non-territorial tactics.

Résumé : D'après les modèles d'optimalité, les mâles pratiquant le lekking qui possèdent des territoires de plus grande qualité devraient mettre plus d'efforts dans le maintien de leur territoire et moins d'efforts dans leurs soins corporels. Nous avons vérifié cette hypothèse selon laquelle les bénéfices sont en corrélation avec les coûts chez des loutres de mer, *Enhydra lutris* (L., 1758), mâles. Nous avons enregistré leur niveau d'activité au cours de suivis ciblés de 10 individus (n = 127). Les territoires de meilleure qualité ont une surface plus grande, plus de ressources alimentaires intéressant les femelles et une proportion plus élevée de marge protectrice le long du rivage et ils permettent aux femelles d'éviter plus facilement le harcèlement des mâles. Contrairement à ce que nous avions prévu, il n'y a pas de corrélation entre la qualité du territoire et les mesures de coût, soit le maintien du territoire (patrouille, interaction) et les soins corporels (alimentation, toilettage). Nous rejetons l'hypothèse qui veut que les bénéfices proximaux soient en corrélation avec les coûts et nous avançons des hypothèses de travail de rechange : (*i*) à cause du taux métabolique élevé des loutres de mer, le succès de la reproduction chez les mâles peut être relié autant aux soins corporels qu'au maintien du territoire; (*ii*) les territoires de haute qualité avec des marges le long du rivage ne requièrent pas d'efforts supplémentaires de patrouille; (*iii*) les mâles ne font pas d'efforts additionnels de maintien de leur territoire avant qu'un plus grand nombre de femelles ne soient en chaleur; ou alors (*iv*) nos mesures saisonnières des bénéfices et des coûts de la territorialité ne représentent pas de façon exacte les facteurs qui affectent le passage des stratégies territoriales aux non territoriales.

[Traduit par la Rédaction]

Introduction

Maintaining a mating territory can be energetically expensive for males (Kodric-Brown and Brown 1978) because it may lead to negative consequences such as (*i*) decreased time available for foraging and resting; (*ii*) increased energy expenditure owing to courtship, mating, and defense activities (e.g., chasing/herding females, patrolling territory boundaries); and (*iii*) risk of injury or death owing to agonistic encounters with conspecifics and predation (Clutton-Brock et al. 1988; Apollonio et al. 1989; Vehrencamp et al. 1989; Gosling and Petrie 1990; Isvaran and Jhala 2000). However, increased access to females and enhanced reproductive success are often positive consequences of territoriality (e.g., Vehrencamp et al. 1989; Rosser 1992; Isvaran and Jhala 2000; Brø-Jorgensen and Durant 2003). Where highly attractive territories lead to increased reproductive success, increased territory defense may prevent loss of the territory to other males (Apollonio et al. 1990; Isvaran and Jhala 2000). Theoretically, males would be predicted to switch from territorial to non-territorial tactics when the costs outweigh the benefits.

Sea otters, *Enhydra lutris* (L., 1758), exhibit resource-defense polygyny (Calkins and Lent 1975; Loughlin 1980; Garshelis et al. 1984; Jameson 1989), a form of territoriality reported for most members of the family Mustelidae

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(Ewer 1973). Female sea otters may be attracted to a territory based on a number of factors, including prey availability, resting areas, protection from wind and waves, accessibility, and total area defended from harassment by other males (Garshelis et al. 1984). Males attempt to mate with females that feed or rest in their territories (Loughlin 1980; Riedman and Estes 1990). Males interact with both single females and females with pups (Pearson and Davis 2005). Males may copulate while guarding females during a consortship, or during brief, opportunistic encounters (Riedman and Estes 1990). Factors affecting successful insemination are undetermined, as are the factors influencing decisions to switch between territorial and non-territorial tactics.

Male sea otters may aggregate in feeding areas up to 150 km distant from areas that attract reproductive females (Kenyon 1969; Garshelis et al. 1984; Bodkin et al. 2000). Therefore, intersexual contact occurs primarily in the context of breeding. Males enter female areas to search for estrous females and establish resource-based breeding territories during non-winter months (Garshelis et al. 1984; Jameson 1989). The peak of breeding occurred during the autumn in Prince William Sound (Garshelis et al. 1984), although evidence of copulations have been reported for all seasons (Jameson and Johnson 1993; Eberhardt and Schneider 1994; Monson et al. 2000). While some mature males maintain year-round territories in female areas (Loughlin 1980; Garshelis et al. 1984), most apparently switch between territorial and non-territorial tactics during the year (Garshelis and Garshelis 1984).

Garshelis et al. (1984) were the first to measure territory quality during the peak breeding season, based on size, degree of shoreline enclosure, entrance accessibility, and food resources at Gibbon Anchorage, Green Island, in Prince William Sound, Alaska. They found territory quality to be positively correlated with proximate benefits, measured in terms of copulatory success. However, they did not measure the potential costs associated with individual variation in territory quality to determine whether benefits outweighed the costs of maintaining a territory. We argue that the cost of establishing a territory prior to the breeding season may be substantial and should be considered in a fuller investigation of the factors influencing male decisions to switch between territorial and non-territorial tactics.

In the present study, we used the territory assessment criteria of Garshelis et al. (1984) to examine the relationship between territory quality and male sea otter behavior prior to the peak of the breeding season. Although we could not assess benefits in terms of copulatory success, we assumed that the physical characteristics of more successful territories identified by Garshelis et al. (1984) would be valid at a different location within the same coastal system, Prince William Sound. We predicted that males holding higher quality territories would spend more time in territory maintenance and less time in body maintenance activities compared with males holding lower quality territories.

Materials and methods

Study site and season

Simpson Bay is a shallow fjord (Gay and Vaughan 2001) located in northeastern Prince William Sound (ca. 60.4°N, 145.5°W). Because of its location, Simpson Bay was not affected by the 1989 *Exxon Valdez* oil spill. It is composed of two arms (northwestern and southeastern) with a total area of ca. 13 km^2. The median width of Simpson Bay is 1.7 km, maximum length is 9.5 km, and maximum depth is 90 m. The seafloor of Simpson Bay is primarily soft sediment with occasional rocky reefs (Gilkinson 2004).

During a historic period of population expansion, Simpson Bay was occupied by male sea otters (Garshelis and Garshelis 1984; Garshelis et al. 1984). During the summer of 2003, Simpson Bay was used by female sea otters and their dependent pups, single females, and adult territorial males. According to bi-weekly censuses of the study site, the number of otters in the study area was 121 ± 12.1 (mean ± SD; N = 5 surveys), which included an average of 29 pups (Pearson and Davis 2005).

The summer field season (16 June to 31 August 2003) was divided into six 8-day monitoring periods that coincided with groups of Earthwatch volunteers who assisted with spotting sea otters and with the logistics of recording data. Territorial males were observed on a regular schedule by dividing the study area into three sections (top of the northwestern arm, bottom of the northwestern arm, and the southeastern arm) and monitoring each section evenly. Observations were conducted from ca. 0900–1830 local time, and an attempt was made to observe each male at diverse times throughout the day. Differences in diel activity have not been found for territorial males in this area (Pearson and Davis 2005).

Individual identification

Applying standard techniques of photo-identification (Würsig and Jefferson 1990), we used nose scars (Foott 1970), other facial features (e.g., skin pigmentation around the mouth, pelage color, broken or worn teeth, vibrissae characteristics), and general location in the study area to find and identify males. Nose scars were present in 63% (19/30) of males (Pearson and Davis 2005). Boat-based observers determined that an otter was a territorial male by the presence of a penile ridge or testicular bulge (visible through binoculars), and of patrolling behavior. Patrolling is a form of locomotion whereby a male swims belly-down with its head out of the water while scanning the surface, presumably for other males and receptive females. Patrolling is a conspicuous male behavior because female sea otters primarily float on their backs or swim submerged.

Observations of the 10 identified males resulted in 69% of the total number of focal follows (N = 183) and 69% of the total observation hours (N = 91.5). Data from individuals that could not be reliably identified or were not sampled at least 4 times were dropped from further analysis in this study.

Focal observations

The observation platform was a 6 m skiff used to follow the otter at a distance of 50–100 m for a period of 30 min. We took instantaneous samples (Altmann 1974; Lehner 1996) at 1 min intervals to record the following activities: forage, groom, interact with other otters, swim, patrol, rest, and other.

Table 1. Adaptation of criteria for assessing relative quality of sea otter (*Enhydra lutris*) territories in Prince William Sound, Alaska.

Attribute	Adapted criteria (this study)	Original criteria (Garshelis et al. 1984)	Rank value
Size (x_1; km^2)	>1.0	>0.3	2
	0.5–1.0	0.15–0.3	1
	<0.50	<0.15	0
Shoreline enclosure (x_2)	Land on two sides	Land on three sides	2
	Land on one side	Land on two sides	1
	Mainly open	Mainly open	0
Accessibility (x_3)	Entrance(s) not blocked by another territory	Entrance(s) not adjacent to another territory	2
	Entrance(s) partially obstructed by another territory	Entrance(s) partially obstructed by another territory	1
	Entrance(s) mostly obstructed by another territory	Entrance(s) totally obstructed by another territory	0
Prey availability (x_4)	Number of females feeding in territory divided by 10*	Number of females feeding in territory divided by 20† (values ranged from 0 to 2.1)	na

*The number of females we observed was half as many as that observed by Garshelis et al. (1984). See Table 2.

†The prey availability attribute was divided by 20 to scale with the other three attributes.

Behaviors were identified based on descriptions in Packard and Ribic (1982) and Calkins and Lent (1975). We defined ‘‘interact’’ as physical contact between two individuals or synchronous behavior by two individuals in close proximity (≤3 m). In our study, interactive behavior took precedence over all other activities. For example, the behavior of a male that was swimming with a female or grooming beside her was coded as ‘‘interact’’, not ‘‘swim’’ or ‘‘groom’’.

Latitude and longitude were recorded at 5 min intervals using a global positioning system. The majority (98%) of these observations were conducted under weather conditions ranging from Beaufort 0–2, 0%–100% cloud cover, and with no-to-light rainfall.

Assessment of territory quality

We adapted and measured the same four attributes of territory quality as Garshelis et al. (1984): size, shore, access, and prey. Ranks of each attribute were coded within a range of 0–2, with higher ranks coding for higher quality (Table 1). Each territory was then rated according to these four attributes as described below.

Territory size was calculated using the minimum convex polygon method (Odum and Kuenzler 1955) in ArcMap™ version 8.3 (Environmental Systems Research Institute, Inc. 1999). Location points used in plotting territory size included those obtained during focal observations of territorial males, as well as those obtained during intensive photo-identification observations conducted separately by Gilkinson (2004) within the study site during the 2003 summer season. Territories ranged from 0.35 to 2.23 km^2, which were approximately 4 times larger than those reported by Garshelis et al. (1984).

We modified our criteria for the shoreline enclosure attribute from that used by Garshelis et al. (1984) because the topography of our study site was a bay on the mainland rather than coves on an island (Table 1). We scored shoreline enclosure on 2 sides as high quality, in contrast to the ‘‘3 side’’ criteria defined by Garshelis et al. (1984).

Accessibility was ranked based on the number of entrances blocked by the territories of other males (Table 1). For example, if a territory was located in the ‘‘dead end’’ of the arm of a bay, it was ranked lower accessibility than one located at the ‘‘mouth of the arm’’. The rational was based on observations that males tended to intercept females entering at the ‘‘mouth of the arm’’.

Because a direct measure of prey availability was not available for Simpson Bay (Gilkinson 2004), we used an indirect approach similar to Garshelis et al. (1984). We assigned a score for ‘‘food availability’’ based on the number of females observed feeding in each territory (Table 1). The logic was that female sea otters would aggregate where food resources were plentiful, being ‘‘better samplers’’ than scientists (Garshelis et al. 1984). Our measures differed from Garshelis et al. (1984) because we counted females during the summer rather than during the winter. At Gibbon Anchorage, males left after the fall breeding season (Garshelis et al. 1984). We believe that the number of females feeding within each territory was a good indication of prey availability because the foraging success rate was 91% in Simpson Bay during the summer of 2003 (H.C. Pearson, A.K. Gilkinson, and R.C. Wolt, unpublished data).

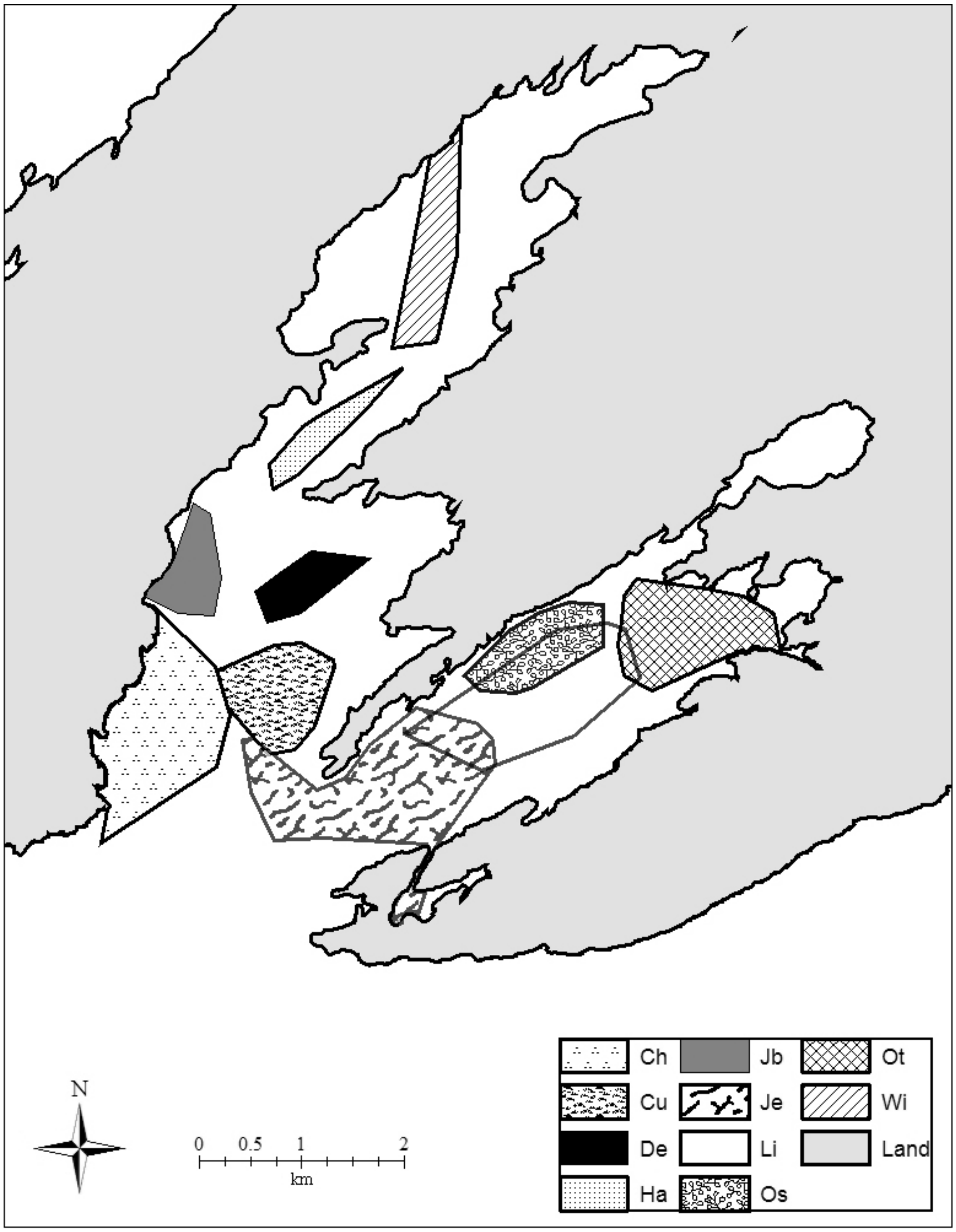
Data analysis

We calculated a summary score for each territory because the four attributes of territory quality were highly intercorrelated. For example, territories at the end of the arms of the bay were ranked high for shoreline enclosure and low for accessibility; they also tended to be smaller than territories patrolled by males at the mouth of the arms of the bay. Therefore, we followed the procedure used by Garshelis et al. (1984) to determine a linear combination of variables that would best describe the orthogonal variation in the data. Principal components analysis (PCA) was used to transform the set of correlated variables into a set of uncorrelated linear combinations (Dunteman 1989; Stevens 1992; Bryant and Yarnold 2003). We used the first principal component to calculate a single score for each territory, based on the weights of the coefficients for each variable:

$$y = 0.37x_1 + 0.32x_2 - 0.25x_3 + 0.34x_4$$

where $x_1, \ldots, x_4$ represented each of the territory quality attributes defined in Table 1. The eigenvalue for the first principal component (eigenvector) was 2.41, representing 60% of the total variance. The total variance explained by the eigenvector was calculated by dividing the eigenvalue by the

Fig. 1. Territories of male sea otters (*Enhydra lutris*) in Simpson Bay, Alaska, during the summer of 2003.



number of original variables and then multiplying by 100% (Bryant and Yarnold 2003).

All statistical analyses were calculated using SPSS® version 12.0 (SPSS Inc. 2003). Descriptive statistics included means and standard deviations (mean ± SD). Kendall's τ was used to test the following bivariate correlations: (*i*) territory quality and body maintenance (% of total instants recorded per individual), (*ii*) territory quality and territory maintenance (% of total instants recorded per individual), and (*iii*) body maintenance and territory maintenance. Statistical significance was determined using a two-tailed α level of 0.05.

Results

Territories were distributed throughout Simpson Bay, covering 68% of the water surface (Fig. 1). Some males switched between territorial and non-territorial tactics during the summer study season. We observed several instances of non-territorial adult males in the study site. For example, during periods when male Ha appeared to be absent from its territory, two different males were observed on three separate occasions in the same territory. In addition, on two occasions within a 4-day period, we observed another male patrolling and interacting with females, but it was not seen again in Simpson Bay. Two other unknown adult males were observed interacting with females, and each male was sighted only once.

Territory quality

High-quality territories had (*i*) large areas, (*ii*) many feeding sites for females, (*iii*) more shoreline enclosure, and

Table 2. Variation in territorial attributes (Table 1) and behavioral measures of costs for territorial male sea otters in Simpson Bay, Alaska, during the summer of 2003.

	Territorial attribute				Behaviors (%)	
Male ID (territory-quality score)	Size	Shoreline enclosure	Accessibility	Prey availability	Body maintenance*	Territory maintenance†
Je (1.8)	2	2	1	0.7	10	77
Ch (1.4)	2	1	1	1.3	33	49
Ot (1.3)	2	2	1	0.5	53	27
Li (1.2)	2	0	1	0.2	59	14
Os (0.9)	1	1	0	0.1	47	25
Wi (0.6)	1	1	2	0.1	48	26
Cu (0.4)	1	0	1	0.1	34	26
Jb (0.1)	0	1	1	0	22	25
De (–0.3)	0	0	2	0	7	80
Ha (–0.4)	0	0	2	0	69	28

*Body maintenance activity was defined as feeding and grooming.

†Territory maintenance activity was defined as patrolling and interacting with female.

(*iv*) more entrances near other territories (Table 2). Territory quality ranged from a low of –0.4 to a high of 1.8 (0.7 ± 0.75). For example, male Je held the highest quality territory at the mouth of the southeast arm, while male Ha defended the poorest quality territory in the middle of the northwest arm of the bay. Territory size ranged from 0.35 to 2.23 km^2 (1.0 ± 0.62 km^2).

Body and territory maintenance activities

Costs of territorial defense varied widely across individuals (Table 2). The percentage of time spent in body maintenance activities ranged from 7% to 69% (38% ± 21%). The percentage of time spent in territory maintenance activities ranged from 14% to 80% (38% ± 23%).

Territory quality was not significantly correlated with the amount of time spent in body maintenance activities (Kendall's $\tau = -0.022$, $n = 10$, $P = 0.93$) or territory maintenance activities (Kendall's $\tau = 0.068$, $n = 10$, $P = 0.79$). The amount of time spent in body maintenance activities was not significantly correlated with the amount of time spent in territory maintenance activities (Kendall's $\tau = -0.341$, $n = 10$, $P = 0.18$).

Two males (Je and De) were outliers in that they allocated much more effort to territorial than body maintenance (Table 2). One defended a high-quality territory and the other a low-quality territory (Fig. 1). The data set was partitioned to exclude these two unusual individuals and correlations were recalculated for territory quality. The correlations still failed to attain statistical significance for body maintenance (Kendall's $\tau = 0.000$, $n = 8$, $P = 1.00$) and territory maintenance (Kendall's $\tau = 0.074$, $n = 8$, $P = 0.80$)

Discussion

Prior to the breeding season at this site, benefits were not correlated with the costs of territoriality. We found no significant relationships between territory quality and amount of time spent in territory or body maintenance activities. Thus, we reject our hypothesis that territory quality was related to time spent in territory and body maintenance activities within the specific ecological context of the present study. Males holding higher quality territories did not spend more time in territory maintenance and less time in body maintenance activities as predicted based on optimality theory.

Our results suggest several alternative working hypotheses that should be tested in the future. First, because of the high metabolic rate of sea otters (Costa and Kooyman 1982), male breeding success may depend just as much on maintaining body condition as maintaining a territory. Second, higher quality territories may not require additional patrolling effort compared with poorer quality territories. Third, when territories are established during the summer months, some males may not expend extra effort in patrolling and interacting until more females come into estrus during the autumn. Finally, territory quality may not be a good predictor of time spent in territory maintenance activities. We will explore the rationale behind each of the hypotheses below.

Metabolic rate and body maintenance

Sea otters have a high metabolic rate, high rate of food consumption, and must groom their fur for thermoregulation in the cold, marine environment. Therefore, male sea otters may not be able to invest as heavily in territory maintenance as other species because a certain minimum level of body maintenance is necessary for survival. If body maintenance drops below this minimum, breeding success may be limited by poor physical condition. Thus, for territorial male sea otters, it may be advantageous to maintain a balance between territory and body maintenance activities.

Patrolling activity

Higher quality territories may not require additional patrolling effort compared with poorer quality territories because a high ratio of shoreline edge is an attribute of higher quality territories. When compared with terrestrial territory owners, however, marine territory owners may spend more time and effort in territory maintenance activities. For example, scent-marking is a form of territory defense used by ungulates such as white rhinoceroses (*Ceratotherium simum* (Burchell, 1817)), Thomson's gazelles (*Gazella thomsonii* Günther, 1884), and hartebeests (*Alcelaphus buselaphus* (Pallas, 1766)). Males of these species regularly scent-mark their territory boundaries while patrolling (Owen-Smith 1977; Gosling and Petrie 1981; Krebs and Davies 1993). Scent-marking is a passive behavior for territory owners to advertise their presence to intruders and may serve to reduce the costs of intrasexual aggression (Gosling 1986). However, scent-marking is impossible in the marine environment, and male sea otters may spend more time patrolling territory boundaries as compared with terrestrial males that use scent-marking in territorial defense.

During the course of the summer, we observed five adult males that did not appear to be maintaining territories, but which still patrolled and interacted with females. In particular, two males occupied the territory of male Ha while he was absent. We believe these to be instances of transient or roaming individuals that opportunistically interact with females as they pass through Simpson Bay. We do not believe them to be territorial because, if these males had remained in the area, they would have been photographically re-identified on the basis of nose scars. Evidence of roaming as an alternative mating strategy has also been reported in male bearded seals, *Erignathus barbatus* (Erxleben, 1777) (Van Parijs et al. 2003). Alternatively, these five male sea otters could have been investigating the area for territory establishment later in the season.

Synchrony of estrous females and territory maintenance

Some studies have found relationships between the peak number of estrous females and time spent in territory and body maintenance activities. Male harbor seals (*Phoca vitulina* L., 1758) spent more time searching for and attracting mates and less time foraging when females came into estrus (Hayes et al. 2004). Male coyotes (*Canis latrans* Say, 1823) exhibited the highest rates of territory defense during and immediately following the breeding season (Gese 2001). For male collared lizards (*Crotaphytus collaris* (Say in James, 1823)), peaks in displaying, patrolling, and interacting coincided with the peak in female receptivity (Baird et al. 2001). In contrast, our study did not reveal similar relationships for territorial male sea otters during the summer, perhaps because this was prior to the period of peak female receptivity.

Unlike some pinnipeds such as Antarctic fur seals (*Arctocephalus gazella* (Peters, 1875)) and Atlantic grey seals (*Halichoerus grypus* (Fabricius, 1791)) where aquatic territories are a secondary or alternative mating strategy (Worthington et al. 1999; Gemmell et al. 2001), the maintenance of aquatic territories is the primary mating strategy for sea otters. Maintenance of aquatic territories is also the primary mating strategy for Weddell seals (*Leptonychotes weddellii* (Lesson, 1826)), where males attract females by defending resource territories around breathing holes in the land-fast ice (Hayes et al. 2004). In contrast, male harbor seals attract females by defending aquatic display territories near female travel corridors — a mating system resembling a “hotspot” lekking system (Van Parijs et al. 1997; Hayes et al. 2004).

Perhaps the greatest obstacle for aquatically mating males is monopolization of females. For example, in land-breeding pinnipeds such as the southern elephant seal (*Mirounga leonina* (L., 1758)), males may control harems of up to 300 females (Modig 1996). However, male control is lost once the female elephant seal enters the ocean. Although male sea otters may use sexual coercion (Smuts and Smuts 1993) to mate with receptive females, females are generally able to move freely through the territories of males.

Measures of territory quality

Theoretically, it should be possible to apply objective criteria to measure and rank the relative quality of territories for species with resource-defense mating systems. For example, the importance of territorial attributes to overall territory quality was similar between our study and that of Garshelis et al. (1984). In both studies, PCA showed size to be the most important component of territory quality, followed by prey availability. However, there are numerous ecological and physical factors that vary in diverse locations even within the same general ecosystem. For example, while Garshelis et al. (1984) found that territories with entrances unobstructed by other territories to be a positive component of territory quality, we found the opposite. We found that higher quality territories had more entrances obstructed by other territories. In our study site, a male may increase the probability that females will enter its territory if the boundaries are adjacent to other territories.

In the present study, we followed the procedure of Garshelis et al. (1984) and measured prey availability indirectly by counting the number of females feeding within a territory. However, conditions may have changed during the two decades since their study. Direct measures of diversity, density, and distribution of prey within each territory would provide a more accurate measure of territory quality. Additionally, more information is needed on the relationship between territory quality and behavior for male sea otters on a diel and seasonal basis.

Several of the issues raised during interpretation of our results are relevant to other studies of the variation within populations of long-lived mammals. Because of the nature of our study site, the sample size is not likely to exceed 10 territorial males. In fact, sample sizes in previous studies of territorial males have also been small, ranging from 2 to 12 individuals (Jameson 1989). However, if studies follow similar criteria for measuring behavior and assessing territory quality, we will obtain a better understanding of how general factors influence male decisions to defend a breeding territory.

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