ARTICLE

A long-term study reveals multiple reproductive behavior strategies among territorial adult male Steller sea lions (*Eumetopias jubatus*)

Pamela Parker and John M. Maniscalco

Abstract: We conducted a long-term study to assess how tenure and territorial behaviors influence reproductive success among male Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)). Copulations by males ($n = 44$) that maintained territories on a rookery in the Gulf of Alaska from 2001 to 2009 were observed using a remote video system. Approximately half of postpartum females copulated with a male in a different territory from where they gave birth. Nearly two-thirds of territorial males with known tenure were unsuccessful in copulating during their first year. Number of copulations for territorial males increased from acquisition year to year 2 with no change in subsequent years. Cluster analysis of tenure and territorial tactic variables for 15 males with observed lifetime reproductive success was used to describe multiple reproductive strategies. Characteristics of the two most successful strategies were the following: (*i*) males typically copulated in their first year, retained the same territories for 3–5 years, and occupied centrally located coastal territories where the highest percentage of females gave birth and (*ii*) males did not copulate until at least their third year and occupied peripheral territories with fewer births for a longer tenure of 7–8 years. Results indicated that lifetime reproductive success was not achieved solely by time on the breeding area; rather, it was achieved from a combination of tenure and territorial tactics.

Key words: reproductive strategies, copulation, pinniped, Steller sea lion, *Eumetopias jubatus*, territorial, tenure.

Résumé : Nous avons réalisé une étude de longue durée afin d'évaluer l'influence des comportements territoriaux et de tenure sur le succès de reproduction des otaries de Steller (*Eumetopias jubatus* (Schreber, 1776)) mâles. Les copulations des mâles ($n = 44$) qui ont maintenu des territoires dans une roquerie du golfe d'Alaska de 2001 à 2009 ont été observées à l'aide d'un système de télévidéo. Environ la moitié des femelles post-partum ont copulé avec un mâle dans un territoire autre que celui dans lequel elles ont mis bas. Près des deux tiers des mâles territoriaux dont la tenure était connue n'ont pas réussi à copuler durant leur première année. Le nombre de copulations pour les mâles territoriaux augmentait de l'année d'acquisition à la deuxième année, les années subséquentes ne montrant aucun changement sur ce plan. L'analyse topologique de variables reliées aux tactiques territoriales et de tenure pour 15 mâles pour lesquels le succès de reproduction à vie était établi sur la base d'observations a été utilisée pour décrire différentes stratégies de reproduction. Les caractéristiques des deux stratégies donnant le meilleur succès de reproduction sont les suivantes : (*i*) les mâles copulent typiquement durant leur première année, conservent le même territoire pendant de 3 à 5 ans et occupent des territoires côtiers centraux où le plus grand pourcentage de femelles met bas, et (*ii*) les mâles ne copulent pas avant leur troisième année au plus tôt et occupent des territoires périphériques comptant moins de mises bas, pendant une plus longue tenure de 7 à 8 ans. Ces résultats indiquent que le succès de reproduction à vie n'est pas seulement lié au temps passé dans l'aire de reproduction, mais dépend plutôt d'une combinaison de tactiques territoriales et de tenure. [Traduit par la Rédaction]

Mots-clés : stratégies de reproduction, copulation, pinnipède, otarie de Steller, *Eumetopias jubatus*, territorial, tenure.

Introduction

A major objective of animal behavior studies is to understand the adaptive significance of behavioral variation (Mayr 1974). Within the same species, multiple reproductive strategies have evolved as a result of individuals competing to maximize their reproductive success (Reynolds 1996). Among mammals, species with extreme sexual size dimorphism tend to have highly polygynous mating systems associated with extreme variance in male lifetime reproductive success (Emlen and Oring 1977). Polygynous males typically provide no parental care, and instead increase their reproductive success by mating with many females (Clutton-Brock 1989; Clutton-Brock and Vincent 1991). A striking feature of many polygynous pinnipeds is a strong skew in reproductive success in which a few males obtain most of the copula-

tions, while the rest have little or no success (Riedman 1990; Hoffman et al. 2003), but see Flatz et al. (2012). Male pinnipeds monopolize receptive females either by occupying significant resources for females (resource-defense polygyny; Riedman 1990; Kiyota et al. 2008) or by limiting the access of other males to females (female-defense polygyny; Sjare and Stirling 1996; Webster and Robinson 1999). Resource-defense polygyny typically involves acquisition and defense of a territory with features that may be attractive to females during times when they are sexually receptive (Kiyota 2005). Female distribution within and among territories could be dependent on availability of pupping habitat (Parker 2006; Kiyota et al. 2008), access to water for thermoregulation (Gentry 1970; Francis and Boness 1991), avoidance of male disturbance through dilution effects to increase pup survival

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(Cassini and Fernández-Juricic 2003), and fitness of territorial males in terms of their reproductive success based on physical body condition, dominance behaviors, or relatedness (Emlen and Oring 1977; Hoffman et al. 2007).

Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) make excellent subjects for investigating reproductive behavior because they are polygynous, highly sexually dimorphic, long-lived (15–20 years; Fiscus 1961), and they occur at high densities during a synchronous breeding season (Gentry 1970; Sandegren 1970). Unfortunately, the most significant research on the reproductive behavior of male Steller sea lions has not been published outside of theses and dissertations (e.g., Gentry 1970; Sandegren 1970; Gisiner 1985; Smith 1988). Males reach sexual maturity between 5 and 7 years of age, but normally do not acquire a territory until between 9 and 13 years of age (Thorsteinson and Lensink 1962; Perlov 1971; Pitcher and Calkins 1981). Breeding season behavior begins when adult males establish territories along topographical lines at rookeries from early to mid-May (Orr and Poulter 1965). The males may continue taking forage trips at sea until the first females arrive during late May, at which time there can be an increase in territorial defense through fighting and boundary displays (Gentry 1970; Gisiner 1985). Females typically give birth to a single pup within 1 week of arrival at the rookery and remain on shore from 3 to 13 days (perinatal period) before returning to sea to forage (Sandegren 1970; Hood and Ono 1997; Maniscalco et al. 2006) and (or) copulating (11.4 days; Gentry 1970). Opportunistic resightings obtained from a small sample size of identifiable female Steller sea lions during their perinatal period indicated that a proportion of females moved away from the territory that they occupied at birth before copulating (Gentry 1970; Sandegren 1970; Gisiner 1985). Copulations occurred throughout the breeding season until mid-July when the following behavioral patterns were evident: departure of territorial males followed by infiltration of postseason males, increased tolerance of juveniles on the rookery by adults, and shifts in the general sea lion distribution towards the waterline (Gentry 1970; Gisiner 1985; Smith 1988).

Copulation frequency has been used as an estimate of male reproductive success based on the assumption that female Steller sea lions copulated once per season over the short time period of estrus (Gentry 1970; Sandegren 1970; Gisiner 1985; Smith 1988); however, the outcome of male reproductive success is ultimately dependent on a female's ability to carry pups to full term and successfully rear them. Behavioral studies of male Steller sea lion reproductive success in the late 1970s indicated that male tenure, territory stability and placement on the rookery, and boundary defense among neighboring males influenced copulation success (Gentry 1970; Gisiner 1985; Smith 1988). Although some territorial males did not copulate in every year, it was believed that copulation success increased annually until at least their third year of territorial tenure (tenure of 2 ± 1.6 years (mean ± SE); Gentry 1970). Yet, the relatively brief durations of previous studies may not provide full representations of male reproductive strategies. It has been suggested that because of the long territorial life of some male Steller sea lions, lifetime tenure and copulation success may be underestimated and studies that span more than 7 years are recommended (Gisiner 1985).

To better understand if multiple reproductive strategies are used by Steller sea lions to achieve reproductive success on a rookery, we conducted a long-term study on the patterns of territorial behaviors of adult males with respect to timing of female estrus. Building upon the knowledge of previous reproductive studies, our 9-year longitudinal behavioral study aimed to (*i*) describe the chronology of the breeding season at a small rookery in the Gulf of Alaska; (*ii*) determine the extent of territory fidelity between reproductive events (parturition and estrus) for individual females; (*iii*) estimate trends in male reproductive strategies that include status, tenure, and territorial tactics (i.e., spatial and temporal use of territories); (*iv*) describe how variation in tenure

and territorial tactics among males may influence their lifetime reproductive success; and finally (*v*) compare our findings to previous estimates derived prior to 1980. We hypothesized that not all males use the same territorial tactics to gain access to females and that rookery tenure is not the only factor to have a substantial influence on long-term copulation success. It seemed plausible that some of the variation in lifetime reproductive success could be explained by multiple behavioral adaptations among territorial males (Baldi et al. 1996; Fabiani et al. 2004).

Materials and methods

Study site and video system

This study was conducted at a low density Steller sea lion rookery on Chiswell Island (59°36′N, 149°34.5′W), located in the northern Gulf of Alaska, during nine breeding seasons from 2001 to 2009. Research staff at the Alaska SeaLife Center (ASLC) operate a remote-control video system at Chiswell Island to observe Steller sea lions in their natural environment on a year-round basis for studies of behavior, life-history parameters, and population dynamics (Maniscalco et al. 2006, 2010; Parker et al. 2008). Over the past decade, there have been approximately 100 adults using the breeding area made of granite rock that was about 40 m × 20 m and 2–15 m above sea level (Parker et al. 2008). Prior to the decline, in July of 1956, there were 1459 adults and 564 pups that occupied an area three times larger (Mathisen and Lopp 1963).

Data collection

Upon arrival to the Chiswell Island rookery each year from 2001 to 2009, adult females and males were photographed and identified by distinct natural markings. Types of natural markings used to identify animals included scars, fungal patches, deep wounds or gouges, discoloration or distinct trailing edges of fore flippers, and missing digits of rear flippers. All adult males and approximately 70% of adult females were uniquely identifiable between years by matching multiple natural markings using relational database of photographs. Up to seven scan samples of identifiable sea lions on the breeding area were conducted daily for 1.5 h duration from at least the hours of 0600 to 2400 throughout the breeding season (Maniscalco et al. 2006, 2010). Scan data included date, time, natural markings used to identify the individual, location on the rookery, behavior state, presence of a territorial male, and absence was noted for all animals that were away from the rookery. Preliminary data collected during 1999 and 2000 indicated that the breeding area consisted of 11 stable territories with boundaries based on natural rock features and topographical lines at the rookery (Fig. 1). During the nonbreeding season of 2005, GPS positions (±0.01 m accuracy) including elevation were obtained at 0.5 m intervals along transects parallel to the surf zone, spaced 1 m apart. Areas of the territories were then calculated using ArcMap® (ESRI (Environmental Systems Research Institute), Inc., Redlands, California, USA). Births were recorded at the time that they were observed or estimated to within ±4 h if not observed and included photographs to determine pupping locations within the male territories. Opportunistic sightings of copulations were recorded from the time the event was noticed until dismount of the male occurred. Copulations were considered successful when intromission was followed by intense pelvic thrusting indicating ejaculation prior to dismount (Gentry 1970; Dewsbury 1972). The timing of estrus was recorded for individual females as the number of days between birth and subsequent observed copulation. Multiple copulations by the same male and female over a 2-day period were included in all analyses. Successful copulations by two different males and a single female were incorporated into the calculation for each male's reproductive success because it was assumed that they had equal chance of siring an offspring. The breeding season was defined to begin with the earliest observed copulation and to end at the approximate

Fig. 1. Aerial photograph of the current breeding area of Steller sea lions (*Eumetopias jubatus*) on Chiswell Island, Alaska, USA, with the 11 main territories outlined. Territorial boundaries were based on aggressive displays among males that occurred at natural rock features and topographical lines within the rookery. The two most reproductive (copulations) territories and the territory with the greatest percentage of births from 2001 to 2009 are labeled. Two sets of two cameras were installed at a 20 ft (6.096 m) cliff above the breeding area of the rookery to maximize observations.
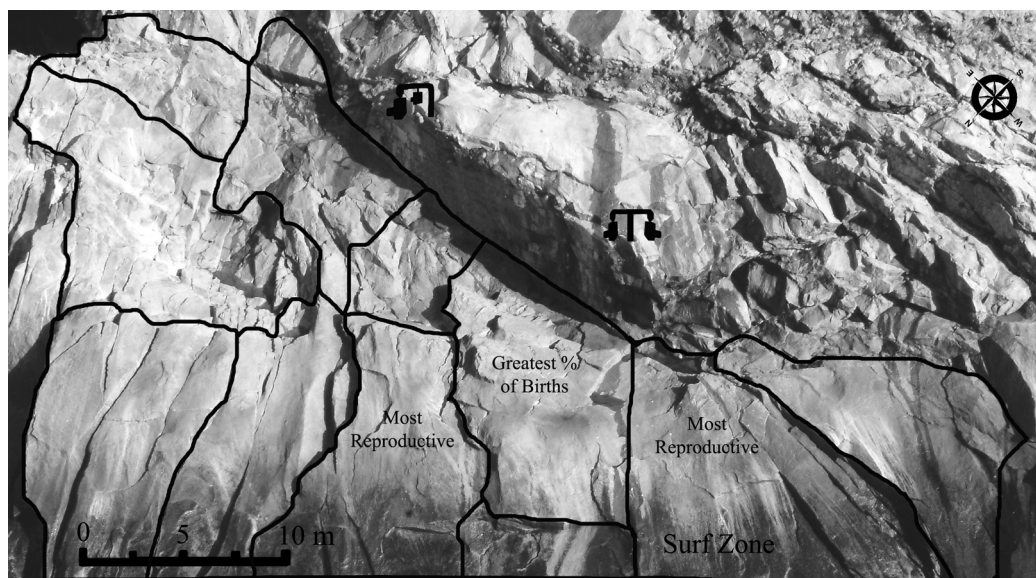
date when territorial males tolerated the presence of subadult males and began to forage at sea away from the rookery. Aggressive interactions among males during the breeding season that resulted in a male being driven out of his territory for more than 24 h were classified as turnover events. Other aggression behaviors were not systematically recorded over the duration of the study and were therefore not included in the analysis. Nevertheless, some of those behaviors provide anecdotal information relevant to this study.

Data analysis

Regression trees are powerful tools for analysis of complex ecological data with the capacity for interactive exploration, description, and prediction of different types of response variables (De'Ath and Fabricius 2000). We conducted regression tree analyses across all years to explore variables that may have affected the distribution of females among the 11 main territories during births and copulations regardless of the individual male present. This analysis was performed using SYSTAT® (Systat Software Inc. 2002) and territory data were grouped relative to the proportion of births and number of copulations observed from 2001 to 2009. Territory variables included in the analyses were centralization of the territory (number of adjacent territories), size of territory (m²), direct access to the sea (coastal, bordering the sea), and for copulations the proportion of births that occurred in each territory. Birthing and copulation locations among the territories at the rookery for individual females were compared to determine the degree of territory fidelity between those reproductive events.

Males inhabiting the breeding area of the rookery at any time during the breeding season were considered either territorial but not observed to copulate (T) or territorial and copulating (CT), whereas those observed on the outskirts or following the breeding season were considered nonterritorial (NT) or postseason territorial (PST), respectively. Previously recorded videos during the breeding seasons at Chiswell Island from 1999 and 2000 were reviewed to obtain photographs that were used to identify adult males and classify them as nonterritorial or territorial. We defined tenure as the number of years observed at Chiswell Island. Data on temporal and spatial use of territories for each male for each year were summarized with descriptive statistics and were

defined as the following territorial tactic variables: date of arrival, time spent holding a territory (days), the proportion of births that occurred while they were territorial, and the percentage of time spent in territories with direct access to sea. Territorial effort (TE) was defined as the percentage of time spent holding a territory during the breeding season relative to peak copulation. A TE score was calculated as $TE = \sum_{i=1}^{n}\left(\frac{D}{|X_i - P|}\right)$, where D is the number of days of the breeding season, X_i is the date present on the rookery, and P is the peak copulation date for all years. The number of observed copulations was calculated annually from 2001 to 2009 for each male. The period of darkness (maximum 5 h) was minimal at this latitude and previous studies reported little copulation activity overnight, suggesting that daylight observations provided a reasonable estimate of copulation success (Gentry 1970; Gisiner 1985). Statistical comparisons were performed using paired t tests or Friedman repeated-measures (RM) analysis of variance (ANOVA) for individuals over years. Graphical and statistical analyses were conducted using R version 2.10.2009-12-10 (R Development Core Team 2009). Significant differences were considered only if $p < 0.05$ and data are reported as percentages and means ± SE unless specified otherwise. Preliminary tenure data for males observed during 1999 to 2000 were incorporated in analyses when the year of territorial acquisition was known. However, data for the remainder of the territorial tactics variables were not obtained in those years and were excluded from analyses.

We estimated lifetime reproductive success based on observed copulations for a subset of males that was observed throughout their entire tenure (≥2 years) at Chiswell Island. Males that were never resighted again meant a termination to their tenure. Cluster analysis was used to explore life-history data and ultimately group males with similar trends for observed territorial tactics and copulation success throughout their tenure. Cluster analysis is a statistical procedure that measures the degree of similarity among individuals based on the relative Euclidean "distance" of the data and forces grouping to explain variability of a selected variable, i.e. observed copulations in our study (Kaufman and Rousseeuw 1990). Mean values for territorial tactic variables and overall lifetime tenure for each individual were used to derive the components of the cluster analysis. Data from the groups of

Fig. 2. Chronology of the breeding season of Steller sea lions (*Eumetopias jubatus*) at Chiswell Island, Alaska, USA, from 2001 to 2009 smoothed with a two-way moving mean. Frequency of birth and copulation events with peaks occurring approximately 10 days apart. Turnover events increased just prior to peak copulation and continued over approximately 10 days.
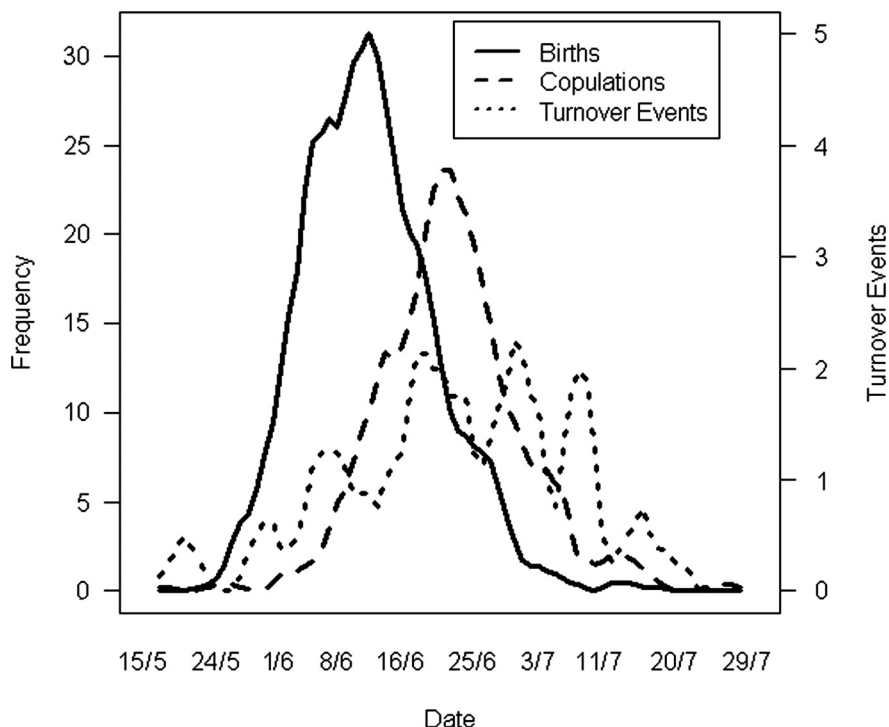
individuals were used to describe the characteristics multiple reproductive behavior strategies. Data are reported as grand means ± SE and percentages for each group.

Permits for this research were issued by the National Oceanic and Atmospheric Administration, National Marine Fisheries Service permit No. 14324 and earlier versions under the authority of the *Marine Mammal Protection Act* and the *Endangered Species Act*. Additional Special Use Permits to conduct this research on refuge lands were acquired from the United States Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge.

Results

Chronology of the breeding season

Ninety-five percent (591/621) of the births (range = 50–78, median = 62 births/year) that occurred on the rookery from 2001 to 2009 had a known location and time within ±4 h. A total of 417 successful copulations were witnessed on the breeding area of the rookery over those 9 years. No copulations were observed on the outskirts of the territories at the rookery. The earliest birth and copulation occurred on 17 May and 24 May, respectively (Fig. 2). Chronology of the breeding season was characterized by a peak birth date of 12 June followed by a peak copulation date of 21 June with turnover events increasing between mid-June and early July. A total of 64 turnover events were opportunistically recorded during 2001–2009. The territorial structure of the breeding season broke down around 15 July when territorial males tolerated the presence of subadult males and the majority of males abandoned their territories. This marked the end of the breeding season and only two births and four copulations were observed after 15 July during all years of this study.

### Distribution of females during births and copulations

On average, births and subsequent copulations were observed for 39% (range = 24%–52%) of the females that gave birth each year at Chiswell Island for a total of 247 from 2001 to 2009. The time between birth and copulation for those females ranged from 4 to

20 days with a span of 11.1 ± 0.13 days (mean ± SE) (Fig. 3). More than half (57%) of females moved away from the territory where they gave birth and copulated with a bull in a different area of the rookery. On average, 9% of copulations per season were with females that did not give birth (range = 0–8 females/year) at Chiswell Island in that year. Only 5% of females successfully copulated with two different males in the same year. Regression tree analyses with data grouped relative to proportion of births indicated that the greatest proportion of births (24%) occurred in the most centrally located territory (four adjacent territories) away from the surf zone (Fig. 1), whereas most copulations (10.0 ± 1.46) occurred in centrally located (three adjacent territories) coastal territories where at least 5% of the females gave birth (Fig. 1). Splits (nonterminal nodes) in these trees minimized the variation within groups and explained 49.7% of the variance in the proportion of births and 46.0% of the variance in number of copulations observed (Fig. 4). Territory size was not an important predictor for proportion of births or number of copulations observed.

Territorial males

A total of 58 different adult males were observed from 2001 to 2009 on Chiswell Island, of which 76% were territorial in at least 1 year and the remainder were not observed on the breeding area during the breeding season. The number of males that held territories per season averaged 14.3 ± 0.5 with 9 ± 0.4 known to have copulated at least once. However, the maximum number of males holding a territory at the same time was 12 (Table 1). On average, turnover events were observed 7 ± 0.6 times/season. The number of copulations (total = 417) observed ranged from 19 to 83 annually with 46 ± 6.2 copulations/season. Territorial males (*n* = 44 individuals) arrived on the breeding area throughout the breeding season with a mean day of arrival of 6 June. Once males arrived, they held a territory for 31 ± 1.5 days. Only 21% of the males maintained a territory over an entire season (53 days). Size of 38 territories (variations of the 11 main territories) ranged from 17.2 to 345.9 m², with 151.6 ± 12.4 m² from 2001 to 2009. The proportion of births

Fig. 3. Density plot for the number of days between births and subsequent copulations for individual female Steller sea lions (*Eumetopias jubatus*) (n = 247) that gave birth at Chiswell Island, Alaska, USA, from 2001 to 2009. The earliest observed copulation was 4 days following parturition with a span of 11.1 ± 0.13 days (mean ± SE).
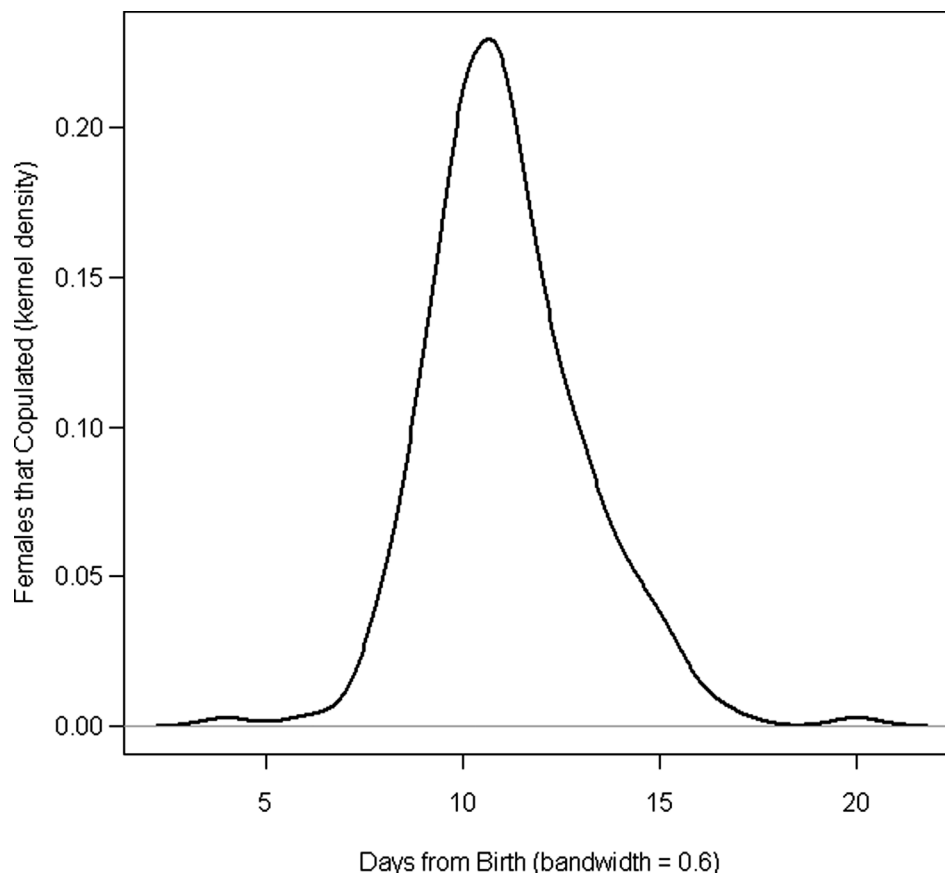
per territory averaged 7.0% ± 0.1% during all years and the number of copulations per male was 3.2 ± 0.4 (range = 1–17).

Male reproductive success

There were 39 males with known tenure and territorial tactics during 2001 to 2009, after removing 5 territorial males identified in 1999 whose tenure was unknown. The majority of males held a territory the year that they were identified and the other 21% invested at least 1 year as a nonterritorial male before establishing themselves on the breeding area (Fig. 5). The longest tenure observed over the duration of this study was 8 years, with 7 years holding a territory. Nearly two-thirds of males that acquired a territory after 2000 (n = 21/33) were unsuccessful in copulating during their first year holding a territory on breeding area from 2001 to 2009 (Fig. 5). There was a significant increase in the number of copulations observed from the acquisition year to year 2 (paired t test; n = 23, mean difference = 3.4, p = 0.001), but no significant change was observed in all subsequent years (Friedman RM ANOVA; p = 0.327).

For 15 males whose entire history on Chiswell Island was known (≥2 years), tenure ranged from 2 to 8 years (4.3 ± 0.5 year). We observed one male mortality during the study period and cause of death was presumed to be abdominal tearing that exposed his intestines. The greatest observed individual lifetime reproductive success was 42 copulations over 6 years (range = 0–42 over 2–6 years, median = 11 copulations). Typically, these males used the same territory in all years; however, there were three individuals that used two different territories and two males that were observed in three or more territories. Results of a cluster analysis including data for tenure and territorial tactic variables indicated

five groups among males with known lifetime copulation success (Fig. 6). We interpreted these groups of males, with similar life histories, to correspond with multiple reproductive behavior strategies that were used to achieve copulation success over a male's lifetime (Fig. 6). After grouping individuals into five strategies, lifetime copulation success varied among strategies ranging from 0.5 ± 0.5 copulations (strategy "*e*") to 30.6 ± 3.2 copulations (strategy "*a*") (Table 2). Characteristics of the two most successful strategies were described as follows: (*a*) males typically copulated in their first year, maintained the same centrally located coastal territories for 3–5 years over the majority of the breeding season where, on average, 14% of females gave birth; (*b*) males were unsuccessful until at least their third year and occupied peripheral territories over 7–8 years during half of the breeding season with access to sea 64% of the time and were present where 4% of the females gave birth. Males of strategy "*c*" had variable tenures ranging from 3 to 6 years and occupied inland territories without access to sea where few females gave birth. They were successful by consistently arriving just prior to peak copulation spending 37% of the time on shore during the breeding season. We hypothesize that males of strategy "*d*" were marginally successful part of their lifetime because they typically exhibited similar territorial tactics as males of strategy "*a*"; however, they copulated after their acquisition year and at times when the percentage of births was half as many. Males of the least successful strategy "*e*" occupied peripheral territories 42% of the time that they were observed and consistently arrived late in the breeding season when copulations were rare (Table 2).

Fig. 4. Regression tree analyses of the (*a*) proportion of births (range = 0%–26%) and (*b*) number of copulations (range = 0–19) observed per territory (*n* = 11) regardless of male Steller sea lion (*Eumetopias jubatus*) present from 2001 to 2009. The explanatory variables were number of adjacent territories (ADJTER; range = 1–4), size of territory (m²), direct access to sea (0 or 1 = boundary that borders the sea), and proportion of births for *b*. These trees explained (*a*) 49.7% and (*b*) 46.0% of the total sum of squares; the vertical depth of each split is proportional to the variation explained.
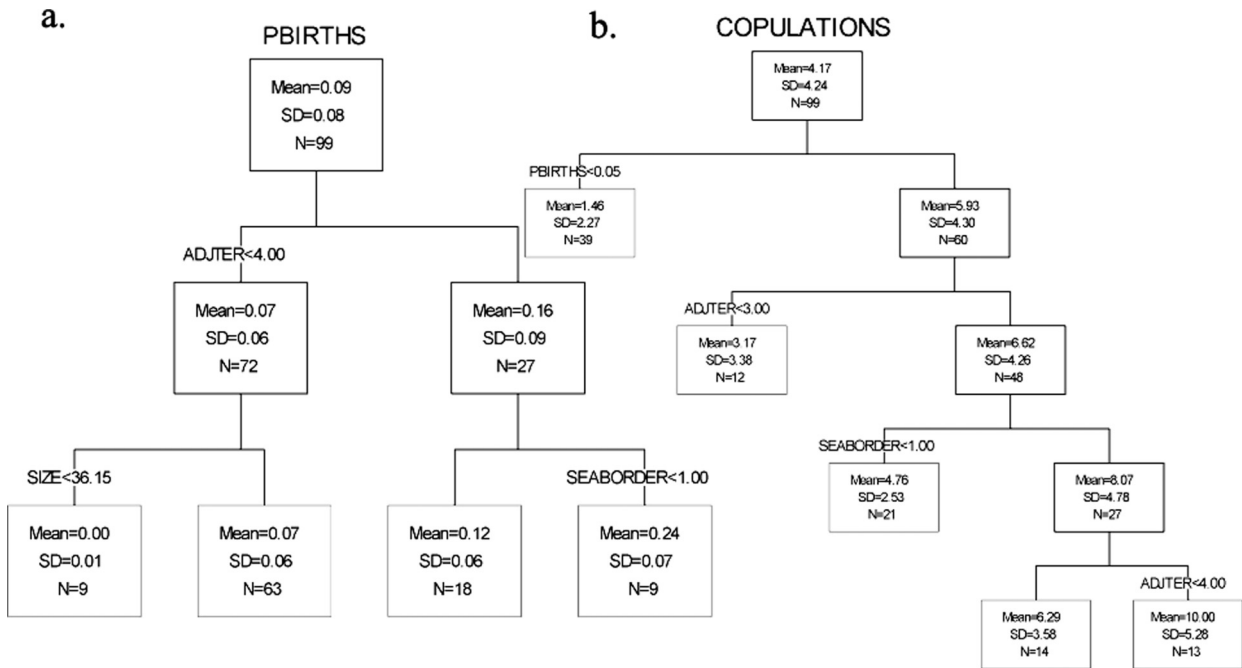
Table 1. Mean (±SE) number and range of nonterritorial (NT), territorial (T), and copulating (C) male Steller sea lions (*Eumetopias jubatus*) (*n* = 58) observed during the breeding season with the percentage identified from a previous year from 2001 to 2009.

	Mean ± SE	Range
Nonterritorial		
During breeding season (NT)	0.8±0.3	0–2
Postbreeding season (PNT)	3.2±0.5	1–5
Territorial (T + CT)	14.3±0.5	12–17
Known in a previous year (%)	81%±2.2%	73%–93%
Copulating (CT only)	9.0±0.4	8–12
Copulated in a previous year (%)	83%±5.9%	56%–100%
Maximum density of males that held territories simultaneously	10.2±0.3	9–12
Turnovers events among territorial males (*n* = 64)	7.1±0.6	5–10
Total observed copulations during a breeding season (*n* = 417)	46.3±6.2	19–83

**Note:** Sample sizes (*n*) are the total number observed throughout the study.

Discussion

Resource-defense polygyny

The chronology of the Steller sea lion breeding season described in this study paralleled early findings throughout the US range with a peak in births during mid-June followed by a peak in copulations in mid-July (Gentry 1970; Sandegren 1970; Gisiner 1985). This pattern among Steller sea lions regardless of rookery location was consistent even though there may be regional variations in the timing of parturition among females (Pitcher et al. 2001). The majority of territorial males arrive at rookeries weeks prior to peak pupping (Gentry 1970; Sandegren 1970; Gisiner 1985; Smith 1988) and is likely under hormonal control (Atkinson 1997).

The long-term maternal care study of females at Chiswell Island provided an opportunity to obtain a large sample size of the time elapsed between birth and copulation. The behavioral onset of estrus as indicated by copulation frequencies in this study occurred at 11.1 days postpartum with little variation. This agrees with earlier studies based on much smaller sample sizes (11.4 days: Gentry 1970; 11.8 days: Sandegren 1970). The distribution of recep-

tive females among territories was an important source of variability in male copulation success in this study as in others (Gentry 1970; Gisiner 1985). Births and subsequent copulations within a male's territory most likely occurred because females stayed near their pups during the time of estrus (Kiyota et al. 2008; Parker et al. 2008). Genetic analyses among northern fur seals (*Callorhinus ursinus* (L., 1758)) (Peterson and Bartholomew 1967) confirmed that the majority (80%) of females copulated with the associated territorial male present subsequent to the year of birth (Kiyota et al. 2008); thus, observed copulations were correlated strongly with estimates of reproductive success. However, just over 50% of the postpartum female sea lions at Chiswell Island moved away from their birthing territories prior to copulating with a territorial male. This supports Gisiner's (1985) findings at Ano Nuevo Island, California, USA, where 46% of 112 females copulated with a male other than the male on whose territory they had been an hour before. This behavior is typically viewed as a female's choice, where females commonly favor mating with dominant males with access to resources (Clutton-Brock 1988,

Fig. 5. Territorial status and copulation success for 39 male Steller sea lions (*Eumetopias jubatus*) with known tenure from 2001 to 2009. Scaled copulation success ranged from 1 to 17 copulations/male. Identification numbers for males with known lifetime reproductive success include the letter associated with their observed lifetime reproductive strategy (*a–e*; i.e., m10b; Fig. 6). Preliminary data for males observed during 1999 to 2000 were included when the year of territorial acquisition was known.
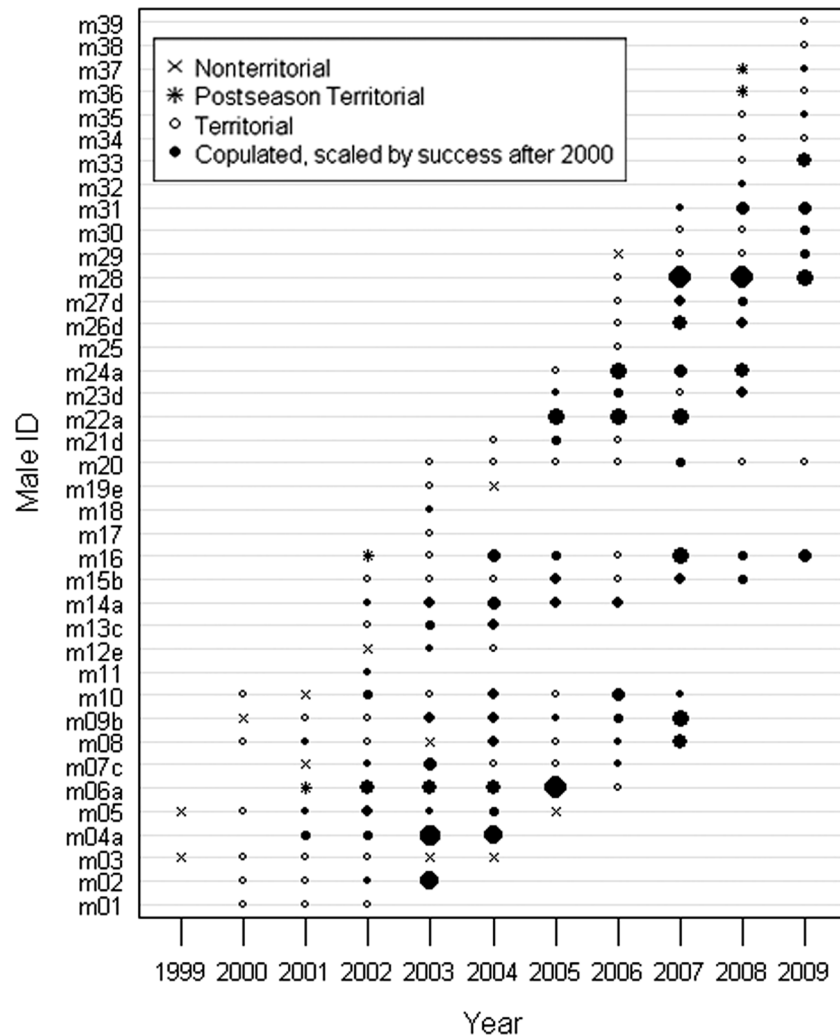
1989) or with males that have potential genetic benefits influencing postweaning survival of their offspring (Hoffman et al. 2007).

Investigating female choice typically required an experimental study or genetic analysis, thus we only speculate why there was variability in female copulatory behavior at Chiswell Island because we had limited funding. For example, we agreed with Gentry's (1970) description of female movement towards the sea for thermoregulation, which potentially occurred between reproductive events. Our analysis of preferred copulation territories indicated that the majority of females copulated in centrally located coastal territories with frequently used pathways to sea. It seemed likely that females were investigated by males in these coastal territories when they departed on their first foraging trip to sea at the end of their perinatal period. Anecdotal observations at Chiswell Island supported this hypothesis because the majority of females returned to their birthing territories following their first foraging trip to reunite with their pups and did not copulate thereafter. We believe male Steller sea lions at Chiswell Island exhibited resource-defense polygyny by defending territories (Hoffman et al. 2006; Kiyota et al. 2008) used by reproductive females that included a combination of pupping habitat (Kiyota 2005; Parker 2006; Parker et al. 2008) and direct access to sea for thermoregulation (Gentry 1970) and foraging trips. It seems plau-

sible that at low-density rookeries, like Chiswell Island, where female sea lions moved freely among territories, it may be advantageous for territorial males to use multiple variations of the most successful reproductive strategy to gain access to females.

Observed copulation success may not always be an accurate proxy for estimating male reproductive success because the relationship between behavioral observations and paternity is not always proportional (Worthington et al. 1999; Lidgard et al. 2004; Pörschmann et al. 2010). Genetic tests of paternity have revealed that some Antarctic fur seals (*Arctocephalus gazella* (Peters, 1875)) and the majority of California sea lions (*Zalophus californianus* (Lesson, 1828)) mate away from their birthing site because their offspring was often sired by males not present at the rookery (Hoffman et al. 2003; Flatz et al. 2012). Females that came ashore but did not pup (Hoffman et al. 2003) or females that entered estrus on their first postpartum foraging trip (Boyd 1991) likely copulated at nearby sites or with males that exhibited alternative mating strategies such as aquatic mating (Francis and Boness 1991). Alternative mating strategies within populations are thought to be evolutionarily stable because different behaviors allow each male type to successfully gain access to females (Sinervo and Zamudio 2001). Behavioral observations combined with genetic studies identified successful alternative reproductive

Fig. 6. Dendrogram of a cluster analysis that grouped male Steller sea lions (*Eumetopias jubatus*) (*n* = 15) with similar life histories into five clusters (*a*–*e*) to explain some of the variability in observed copulation success at Chiswell Island, Alaska, USA, from 2001 to 2009. Mean values for territorial tactic variables (listed in Table 2) and overall lifetime tenure for each individual were used to derive components of the cluster analysis. Clusters (*a*–*e*) were referred to as multiple lifetime reproductive strategies used by males to achieve copulation success over their lifetime.
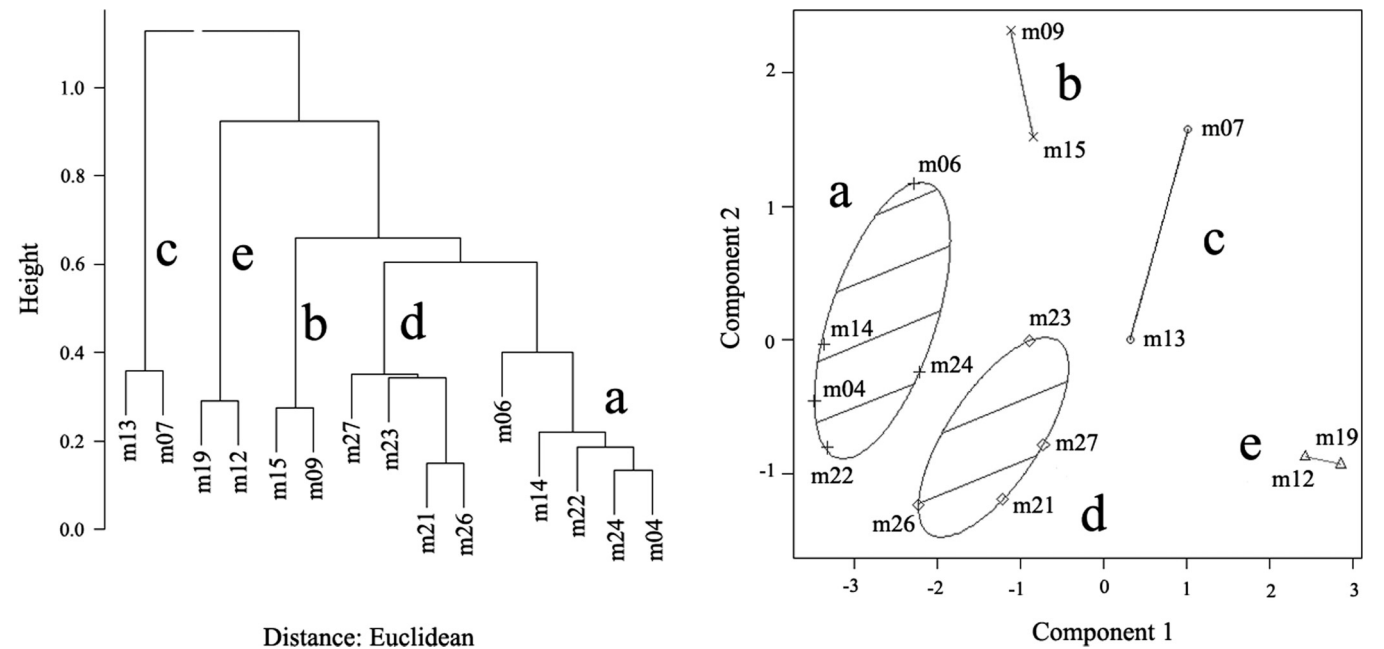
Table 2. A summary of the characteristics of tenure and territorial tactic variables for male Steller sea lions (*Eumetopias jubatus*) with similar lifetime reproductive strategies (*a*–*e*) that were described at Chiswell Island, Alaska, from 2001 to 2009.

Strategy	*n*	Year of first copulation	Tenure (year)	Territorial (%)	No. of adjacent territories	Access to sea (%)	Territorial effort (%)	No. of births/male (%)	Total copulations
a	5	1	4.0±0.6	97	3.3±0.2	100	77	14	30.6±3.2
b	2	3.5	7.5±0.5	94	2.8±0.5	64	58	4	17.0±6.0
c	2	2	4.5±1.5	92	2.8±0.3	0	37	3	7.5±0.5
d	4	2	3.3±0.3	100	2.9±0.5	88	69	8	7.7±1.9
e	2	0	2.5±0.5	42	1.7±0.7	58	5	0	0.5±0.5

Note: The most successful strategies were *a* and *b*, which had the greatest number of copulations. Sample sizes (*n*) are the number of males that exhibited each strategy. Data are reported as grand means ± SE and percentages per group of individuals following a cluster analysis. The "year of first copulation" column reports medians and was not included in the cluster analysis. The "territorial" column denotes the percentage of time that males held territories in their lifetime, whereas the "territorial effort" column was the percentage of time spent holding a territory during the breeding season relative to peak copulation.

strategies among nonterritorial male pinnipeds such as the following: (*i*) interception or sneak copulations by peripheral males outside the typical breeding area (northern elephant seal, *Mirounga angustirostris* (Gill, 1866): Le Boeuf and Mesnick 1991), (*ii*) aquatic copulations observed among terrestrial-breeding pinnipeds (California sea lions and Juan Fernández fur seals (*Arctocephalus philippii* (Peters, 1866)): Francis and Boness 1991), and (*iii*) female stealing, which has only been widely reported in northern fur seals (Gentry 1998; Kiyota et al. 2008). It was assumed that these types of alternative mating strategies were not prevalent in Steller sea lions because all reported copulations occurred within terrestrial territories at rookeries (Gentry 1970; Sandegren 1970; Gisiner 1985; Smith 1988; this study).

We assume that a combination of the above scenarios likely occurred among the sea lions at Chiswell Island. We observed at most 50% of the copulations with postpartum females and a much smaller proportion of copulations with females that did not give birth in a year of observation. Yet, 95% of the time females copulated with only one territorial male, which is greater than the 85% observed at Ano Neuvo Island (Gentry 1970; Gisiner 1985). Copulations did not occur on the outskirts of the territories at the rookery or in the surrounding sea as indicated by previous studies on Steller sea lions (Gentry 1970; Gisiner 1985). These observations

suggested that for males, defending preferred habitat appeared to be the optimal way to access reproductive females. However, some of the copulations must have occurred somewhere other than the rookery. Many females that do not give birth in any given year are not observed on the rookery (Maniscalco et al. 2010) and therefore must copulate elsewhere if they give birth in the subsequent year. Using a similar remote video system, we recorded opportunistic observations of successful copulations at nearby haul-out sites commonly used by female Steller sea lions for resting and nursing juvenile offspring during the breeding season. Even though these haul-outs were not part of this study, it is worth noting that the territorial behavior we witnessed was consistent with that observed at the Chiswell Island rookery. Therefore, if maximizing access to females was the driving force behind male reproductive success, then establishing a territory at any site used by reproductive females during time periods associated with estrus could be successful, especially when a small but highly competitive proportion of the population of males breeds at rookeries.

Territory acquisition, tenure, and copulation success

In species like the Steller sea lion, copulation success was expected to correlate strongly with a male's competitive ability to

defend and maintain a territory throughout the breeding season and over their lifetime (Gentry 1970; Hoffman et al. 2003). Intra- and inter-annual patterns of aggressive interactions among neighboring territorial males have been well described at other Steller sea lion rookeries (Gentry 1970; Gisiner 1985; Smith 1988). At Chiswell Island, we observed that 24% of the males never acquired a territory. Of those that did acquire a territory, only 21% spent at least 1 year on the periphery of the rookery where it was common to rest amicably side by side. This figure was much less than the 50% estimated over a 7 year time span at Ano Neuvo Island (Gisiner 1985). Eventually, some peripheral males obtained post-breeding season territories by defeating resident males when few or no females are in estrus (Gisiner 1985). Aggressive interactions that resulted in temporary or permanent displacement of a territorial male were typically captured because of the increased level of alertness among the group of sea lions. At Chiswell Island, turnover events occurred more frequently following peak copulations as also described by Gisiner (1985). Surprisingly, in the year following this type of turnover event, we often observed that the defeated male arrived first and reclaimed his territory. Some males that were postseasonal for multiple years were successful in obtaining the adjacent peripheral territory. In some cases, a new challenger male defeated a resident male that occupied a centrally located coastal territory prior to peak pupping, which ultimately terminated that male's tenure and implied reproductive death. By the third week in July, the territory structure broke down, postseason males tolerated subadult males and juveniles on the rookery, and the resting spots of females shifted towards the waterline (Gentry 1970; Gisiner 1985; Smith 1988; this study).

In any year, a minimum 73% of the territorial males returned to Chiswell Island. Although the majority of males held a territory the year that they were identified, nearly two-thirds of males at Chiswell Island were unsuccessful in copulating during their first year holding a territory. Only 60% of males copulated, on average, each year from 2001 to 2009, which was slightly less than the 75% reported at Ano Neuvo Island (Gisiner 1985). As expected, once a male acquired a territory, copulation success increased in the following year (Gisiner 1985; Hoffman et al. 2003). However, this trend did not continue but was maintained throughout a male's tenure, indicating that tenure was not the only avenue for achieving greater lifetime reproductive success. It was thought that territorial males typically arrive earlier each year of their tenure and stay later in the breeding season (Gisiner 1985), whereas we observed that males were relatively consistent once they achieved copulation success, except when termination (turnover) occurred during the early breeding season.

Evidence for multiple reproductive strategies

Based on behavioral observations of territorial males in previous studies, it was unclear if individuals adopted various territorial tactics or used multiple reproductive strategies to increase their reproductive success at rookeries. The long-term nature of the present study at Chiswell Island allowed us to accurately estimate lifetime tenure and reproductive success compared with previous studies of male Steller sea lions that were shorter in duration. We observed a greater tenure of 4.3 ± 0.5 years compared with 2.0 ± 1.6 years estimated by Gisiner (1985). One Chiswell Island male with 8-year tenure exceeded the maximum estimate of 7 years, yet the greatest lifetime reproductive success of 42 copulations over 6 years was similar to 68 copulations over 7 years. As observed elsewhere (Gentry 1970; Emlen and Oring 1977; Gisiner 1985), males at Chiswell Island exhibited high variance in lifetime reproductive success with few males obtaining the majority of the copulations, while the rest had little or no success. Behavioral studies of male Steller sea lion reproductive success in the late 1970s indicated that male tenure, territory stability and placement on the rookery, and boundary defense among neighboring males influenced copulation success (Gentry

1970; Gisiner 1985; Smith 1988). Until this study, the degree of variation in territorial tactics among males was unknown and it was not understood that there were multiple reproductive behavior strategies that males used to achieve reproductive success.

Previous studies consistently concluded that the most successful males generally reoccupied the same territory each year. This was based on their observations that defeated resident males persistently attempted to regain their territory in that year, and when they unsuccessful, they were not observed in any year thereafter (Gentry 1970; Gisiner 1985). Their observations of this trend most likely represented males with lifetime tenure and territorial histories similar to strategy "a" males observed at Chiswell Island. The most successful males copulated in their acquisition year and maintained the same centrally located coastal territories for 3–5 years over the majority of the breeding season when the highest percentage of births occurred in that territory. We speculate that these males were likely the most "fit" based on territory selection at a rookery not body size or age. Our results go along with long-term data among Antarctic and northern fur seals where the greatest reproductive success was achieved through territorial site fidelity in the center of female aggregations especially during peak estrus (Kiyota 2005). Furthermore, male South American sea lions (*Otaria flavescens* (Shaw, 1800)) copulated 10 times more by defending territories with permanent tide pools where reproductively receptive females concentrated as a result of extreme thermoregulatory constraints (Campagna and Le Boeuf 1988). Contradictory to previous studies, our long-term study showed that males with the longest tenure were not the most reproductively successful. Males with the longest tenure (strategy "b") achieved reproductive success by adapting each year to different social and spatial compositions on the rookery. These males initially copulated in their third or fourth year, typically held two adjacent peripheral territories throughout their tenure, and were most likely successful when the distribution of females was less concentrated in the center of the rookery such as years when summer storms occurred and females gave birth at greater elevations (Parker 2006). Gisiner (1985) alluded that a few individual's territories changed from year to year by either expanding the original territory or movement to an adjacent territory (ultimately towards the center of the rookery). It is probable that he observed males that exhibited strategy "b" having variable territories throughout their tenure. Notably, we did not see any males move to a completely different part of the rookery throughout their tenure (Gisiner 1985), whereas Hooker's sea lions (*Phocarctos hookeri* (Gray, 1844)) often established multiple territories throughout the breeding season as a response to movement of female aggregations down the beach (Robertson et al. 2008).

Males of strategy "c" held inland territories without access to sea where few females gave birth, but were successful by consistently arriving just prior to peak copulation. These males could have arrived earlier in the breeding season in consecutive years to increase their reproductive success but did not. This indicated that when a strategy was successful, males did not stray much from their previous experience. Males of strategy "d" typically spent 1 year defending a territory before they successfully copulated. Their moderate success (nearly four times fewer) during their short tenure was attained by occupying preferred territories similar to strategy "a". Males that arrived consistently late in the breeding season, when few copulations occurred, and occupied coastal territories were the least successful over their lifetime (strategy "e").

Variation among male Steller sea lion lifetime reproductive success was likely the result of their adaptability to a variety of social and topographic settings. Our results indicate that the greatest lifetime reproductive success was not achieved solely by the number of years spent at the rookery. Rather, reproductive success was achieved from a combination of tenure and territorial tactics such as the method of initial territory acquisition and location of that

territory relative to the distribution of receptive females. In years of low food availability, length of perinatal period may decrease and cause more females to move away from their birth territories towards coastal territories prior to copulation. Alternatively, increasing summer storms would disperse pre- and post-partum females into territories with greater elevations away from the surf zone (Parker 2006). Both of these scenarios would alter lifetime reproductive success for individuals; therefore, the observed strategies could potentially be restructured in order of most successful.

Our long-term study provides new insights into the life-history patterns of male Steller sea lion behavior and contributes new concepts to the study of animal behavior in general. Male territorial systems exhibit significant variation that likely makes them adaptable to changes on both large and small spatial scales. Different terrestrial sites such as haul-outs used by females during nonbreeding years or larger rookeries with varying topography would further diversify male breeding tactics and provide additional material for study. Therefore, the ultimate breadth and significance of male pinniped breeding behavior may be best understood through continuing studies that encompass both large spatial and long temporal scales.

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