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RESEARCH

Territoriality in adult male sub-Antarctic fur seals at Gough Island

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Abstract
We analysed unpublished data on territory size and tenure in adult male sub-Antarctic fur seals *Arctocephalus tropicalis* recorded at Gough Island, Southern Ocean, during the 1975/76 austral summer breeding season. Adult males (n=15) remained on their territories for between 35–56 days (mean 45.4±6.7 days). Territory size during the peak breeding season was 21.9 m^2 on average (n=42), but when partitioned by beach type, average territory sizes were 13.8 (n=9), 20.1 (n=17) and 28.3 m^2 (n=16). Both territory tenure and territory size fall within the reported range of values established in fur seal species which hold territories on land as the predominant male reproductive strategy. We highlight numerous confounding factors that impact comparative studies which should be considered when interpreting theoretical, conceptual, and modelling approaches about territorial behaviour in otariids.

Keywords Adult males · Breeding season · Beach types · Fur seals · Territory size · Territory tenure

Introduction

Sub-Antarctic fur seals (SAFS) breed on Gough Island (40°19′ S, 9°57′ W) in the South Atlantic Ocean (Hofmeyr and Bester 2018). SAFS are polygamous, colonial breeders with adult males defending territories during the austral summer (Bester 1981) on beaches where adult females gather, give birth and mate over a highly synchronised period of approximately six weeks (Bester 1981, 1995). Adult male numbers ashore peak in December (Bester 1981), when fur seal males of various species typically engage in highly ritualised aggressive interactions (Rand 1967; Peterson 1968; Stirling 1971; Miller 1971, 1975). Aggressive encounters between adult males commence in early November, and last to early January (Bester 1981, 1990), a result from seasonally high levels of the reproductive hormone testosterone (Bester 1990; Negro et al. 2010).

Otariid mating systems are classically characterized in terms of male competition and polygyny, although alternative male strategies and female choice also play a part (Miller 2018). Territoriality and dominance hierarchies aim to improve the adult male's reproductive advantage (Stirling et al. 1993). The outcomes of territorial disputes amongst male fur seals to enable access to mates are governed by many factors which include, amongst others, the position of territories on a beach, e.g. providing access to water and shade (Carey 1991; Francis and Boness 1991; Bester and Rossouw 1994), its varying physiognomy (e.g. Stirling 1970, 1971; Miller 1975, 2018; Bester 1982a, b; McCann 1980; Campagna 2018) and male fighting tactics (Miller 1971; Stirling 1971; Bester et al. 2024).

In this study, we analysed unpublished data on territory sizes and tenure collected in summer 1975/76 at Gough Island (Bester 1977) to contribute to the need for descriptive (including quantitative) comparative studies required for interpreting theoretical, conceptual, and modelling approaches about territorial behaviour in otariids (Miller 2018; Bester et al. 2024).

Material and methods

Study area

Gough Island (40°19′ S, 9°57′ W) in the South Atlantic Ocean (Fig. 1) supports the largest population of SAFS

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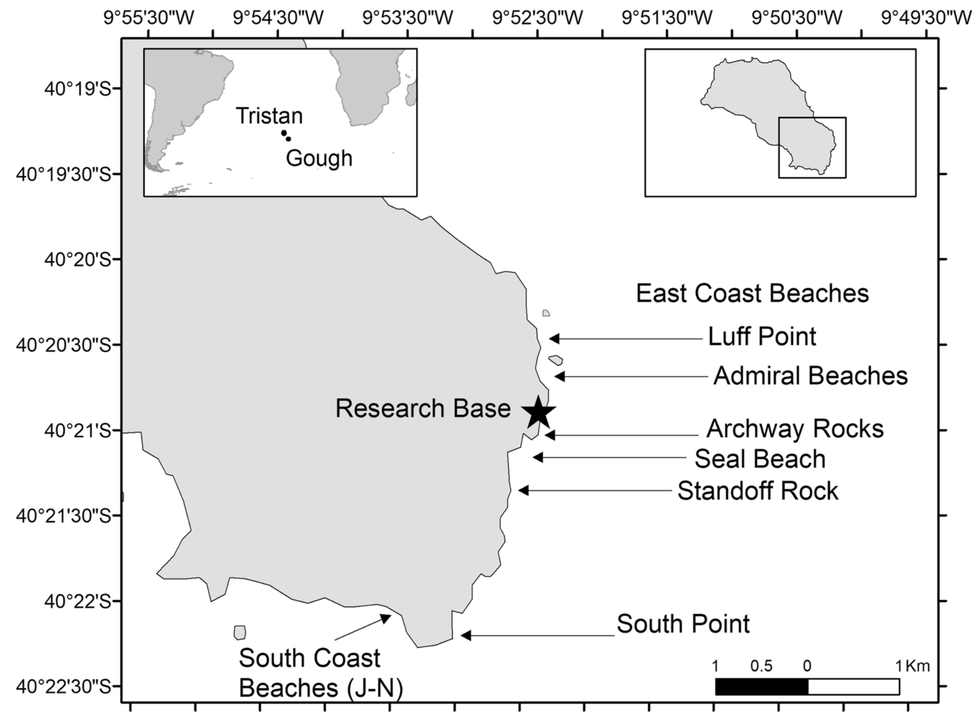

Fig. 1 Map of South Atlantic Ocean showing the location of Gough Island and the study locations on East Coast and South Coast beaches mentioned in the text

(Hofmeyr and Bester 2018). During the breeding season, SAFS variously use different locations on Gough Island as established breeding, breeding, non-breeding and idle colony sites (defined in Bester 1982a) depending on the beach physiognomy. We visited a number of beaches on the South East Coast of the island (Fig. 1) weekly during the 1975/76 breeding season to census the fur seal population (Bester 1981) and to carry out a behavioural study on fighting tactics (Bester et al. 2024), time budgeting and activity patterns (Bester and Rossouw 1994), including adult male territory sizes and tenure (Bester 1977). We calculated adult male territory sizes and tenure for Seal Beach (eastward facing, non-breeding, intermediate type rocky beach), South Point Beach (eastward facing, breeding, jumbled rocky beach on the northern edge of South Point) and Waterfall Cove (southward facing, breeding, jumbled rocky beach designated 'J'). These beaches are identified in Fig. 1, and depicted in Plates 1(b) and 2(a) in Bester (1982a).

Recording of territorial male territories

Identification of adult male SAFS followed Jones et al. (2019). We established the presence and identity of each individual adult male using morphological characteristics, scars, wounds or distinctive colouration variously using 7 × 35 (wide angle) and 7 × 42 binoculars (when afar) or the naked eye (when close) on each visit.

We recorded territory tenure of individual adult males ($n = 15$) at South Point Beach and Waterfall Cove (Fig. 1). We calculated time of tenure from (a) the approximate time they established territories during the latter half of November when uniformly large territorial males showing rigid territorial maintenance behaviour start arriving (Bester 1977, 1981) to (b) their assumed departure shortly after the last census that they were present, to before the subsequent census.

Territory size for a number of territorial males ($n = 42$) was calculated for Seal Beach ($n = 9$), South Point Beach ($n = 17$) and Waterfall Cove ($n = 16$). We identified the extent of their territories through the geographical limits of the resident males' boundary threat displays (see Stirling 1970, 1971; Miller 1975, 2018; Bester 1977) directed towards neighbours/trespassers during territory establishment and maintenance leading up to the peak breeding season (6–13 December 975). By this time, habituation to neighbouring males had usually occurred (Gentry 1975; Bester 1977; McCann 1980; Miller 2018) and territorial borders were set. Beaches which had been evaluated according to the relative contribution by differently sized and shaped stones to its general relief (Bester 1982a), were gauged for its likely impact on territory sizes (Bester 1977). At the end of the breeding season when it was safe to access the three beaches, we measured territory size using reference sketches/maps of territory lay-out made at various times during the season (Miller 1971; McCann 1980; Francis and Boness 1991).

Statistics

Statistical analyses were conducted with R version 4.3.1 (R Core Team 2023). Summary statistics of territory sizes (S1) are presented (Table 1). ANOVA tested for a significant difference between 3 colonies, followed by multiple comparisons with Bonferroni correction (using modified significance level of 0.05 / 3 = 0.017) to determine specific differences between the various groups (S1). Box plots were prepared to visualize the results (S1).

Results and discussion

Territory tenure

The fifteen adult males remained on their territories for between 35–56 days (mean 45.4±6.7 days). The one male for which the exact date of territory procurement (when he dislodged a resident male) was known, stayed on site for between 48–56 days. This is similar to that recorded for two (50 and 58 consecutive days) *A. australis* males (Vaz-Ferreira 1956). The approximate duration of territory tenure (mean 36±9.7 days, range 21–54 days, *n*=16) in *A. forsteri* (Stirling 1971) was somewhat shorter, and in *A. gazella*, considerably shorter than in *A. tropicalis*. The mean period of tenure in *A. gazella* bulls seen to copulate (*n*=13) was 34.3±9.0 days and for those bulls not seen copulating (*n*=18) it was 12.4±12.3 days (McCann 1980).

Important determinants of period of tenure in territorial male otariids (McCann 1980) include body size (condition), climate (warm versus cold) and duration of mating period (long in low latitude versus short in high latitude species). The differences in duration of mating period between high latitude and low latitude species are maintained even on mid-latitude, temperate islands where such species occur in sympatry (e.g. Kerley 1983). Furthermore, male fur seals are not rigidly tied to territories and territorial behaviour, and may change locations (Carey 1991; Bester and Rossouw 1994; Miller 2018) and/or resort to the sea (Warneke 1966; Rand 1967; Francis and Boness 1991; Bester and Rossouw 1994) or shade (Carey 1991; Bester and Rossouw 1994) during times of excessive heat loading. Shade is not actively sought by territorial male *A. forsteri* (Miller 1971), but they follow females that seek shade (Carey 1991). Absences in adult male *A. philippii,* usually in the hot afternoons (Francis and Boness 1991) might be lengthy (mean=44.5 min, range 14–116 min). Although individual males always returned within 2 h, sometimes males departed two or three times on hot afternoons after having dried. In *A. forsteri*, absences might even last days (Miller 1971). In addition, thermoregulatory considerations related to the degree of exposure to prevailing climatic conditions even influence the selection of beaches for establishing breeding colonies (Bester 1982b).

Mating success was positively correlated to duration of tenure (days) on land in a high latitude (cold climate) fur seal such as *A. gazella* (Arnould and Duck 1997). However, heat loading conceivably influences the duration of time that land-based territorial males have access to fur seal females in mid-latitudes which may affect reproductive success (through reduction in copulation frequency). In the mid-latitude *A. australis*, males with satellite reproductive tactics, i.e. males that defend very small territories that are located in areas commonly used by females, have a higher average breeding success than the dominant and most competitive territorial males (Franco-Trecu et al. 2014). Additionally, in the low latitude Juan Fernandez fur seal (*A. philippii*), the average male holding an aquatic territory (the only fur seal species that does so) achieved as many copulations as did the average land-locked or shoreline male (Francis and Boness 1991). Duration of tenure therefore does not necessarily translate into enhanced reproductive success.

Nevertheless, our lack of daily visits to the two breeding colony beaches this study likely resulted in overestimation of mean tenure time by a number of days compared to another mid-latitude, temperate climate fur seal, *A. forsteri*. Despite this shortcoming, calculated tenure in *A. tropicalis* remains largely within the range of tenure in the other mid-latitude fur seals (*A. forsteri* and *A. australis*) which are subjected to similar climatic conditions.

Table 1 Territory sizes of adult male sub-Antarctic fur seals measured at colonies on three beaches during the peak in the austral summer breeding season of 1975/76 at Gough Island

Colony	Territory size (m^2) Mean	Range	S.D	*n*
Seal Beach	13.8	8.5—21.0	2.69	9
South Point Beach	20.1	5.0–41.5	4.24	17
Waterfall Cove	28.3	12.5–63.0	21.07	16
All	21.9	5.0–63.0	12.3	42

Territory sizes

Overall, average territory sizes of *A. tropicalis* males during the height of the breeding season on Gough Island was 21.9 m^2 (*n* =42), and comparable to the 23.0 m^2 recorded for *A. forsteri* (*n*=12) by Gentry (1975). However, when partitioned by beach type (Table 1), average territory sizes were 13.8, 20.1 and 28.3 m^2 for Seal Beach (*n*=9), South Point Beach (*n*=17) and Waterfall Cove (*n*=16), respectively. At Seal Beach, an intermediate beach type (see Bester 1982a), the territorial males interacted with all arriving/departing seals that invaded their space, including subadults of both sexes (Bester 1977). Seal Beach is a non-breeding colony site by definition (Bester 1982a) and a maximum of four adult females were found present at any one time, of which only one produced a pup at this site. The other two jumbled rocky beaches were breeding colony sites (Bester 1982a) each with a minimum of 60 adult females, yielding at least 35 pups by the end of the breeding season (Bester 1977).

Territory size (Table 1; S1) was significantly different amongst the three beaches (ANOVA Test statistic=4.7650, df1=2, df2=39, p-value=0.014<0.05) with territory size comparison between Waterfall Cove (relatively large territories) and Seal Beach (relatively small territories) significant (Multiple comparisons with Bonferroni correction Test statistic=2.9767, p-value: 0.005 <0.017). This is the likely result of the paucity of adult females at Seal Beach which presumably stifled territorial behaviour. *Arctocephalus philippii* territory sizes also vary depending on the situation, where average territory size was 43 m^2 and 18 m^2 for shoreline (n=11) and land-locked (n=18) males, respectively (Francis and Boness 1991). The distribution of territories in *A. forsteri* (Miller 1971; Cary 1991) and *A. australis* (Franco-Trecu et al. 2014) was also modified by the presence of females. The absence of females from territories provides conditions that favour temporary thermoregulatory induced departures by land-locked males (Rand 1967; Gentry 1973; Bester and Rossouw 1994), and occasionally by shoreline males as well (Francis and Boness 1991). This happens when thermoregulatory behaviour overrides reproductive activities (Whittow 1987), which may also result in the maintenance of smaller territories in the absence (temporary or otherwise) of females (this study).

In *A. gazella*, continued arrival of successful males on the congested breeding beaches decreased mean territory size from about 60 m^2 in mid-November to 22 m^2 in December (McCann 1980) on the predominantly open, low profile shingle beaches where few visual cues for territorial demarcation existed (Bonner 1968; McCann 1980). By contrast, the effective territorial space use (566 m^2) at Waterfall Cove, derived from the maximum number of territorial males hauled out at any one time during the peak breeding season ($n = 20$) and the mean territory size (28.3 m^2), fell short by 474 m^2 of the full measured extent of the beach (1,040 m^2). This unused area constitutes mostly inaccessible topographical features which serve as visual cues for delineation of territory boundaries, and would influence (limit) the number of territorial males which can occupy the site, and therefore affect territory sizes.

Conclusions

To address the ways in which adult male fur seals promote their reproductive fitness during the breeding seasons, the dual role of territory size and tenure must be considered. Although both territory tenure (± 45 days, likely overestimated) and territory size (±21.9 m^2) in adult male SAFS fall within the range of values established for other southern fur seal species, it is clear that numerous factors affect reproductive success of fur seal males. In fur seal species where holding territories on land is the predominant male reproductive strategy, territory size and tenure are variously influenced by (a) beach physiognomy (size and physical structure), (b) beach orientation (windward/leeward), (c) access to water and shade, (d) latitude (high, mid, low) and climate (cold, temperate, warm), (e) observation timing (early, peak, or late part of the breeding season), (f) observation frequency (hourly, daily, weekly, etc.) which impacts accuracy of observations on tenure, and (g) female presence, number, and distribution over colony sites. The role of all these factors needs to be evaluated in comparative studies to interpret theoretical, conceptual, and modelling approaches about territorial behaviour in otariids.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-024-03325-x.

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Author contributions MNB planned the study, and together with GJR, recorded all the observations. MNB sourced relevant scientific literature, drafted, read, edited and approved the manuscript.

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Data availability All territory size data generated and analysed during this study are included in this article and its supplementary information file. The original data used for territory tenure calculations are no longer available, and the summary calculations were taken directly from Bester (1977).

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval Field procedures in 1975/76 were approved by the Director-General, South African Department of Transport, under advice from the South African Scientific Committee for Antarctic Research, pursuant to the provisions of the South African Sea Bird and Seals Protection Act, 1973 (Act 46 of 1973), and the Convention for the Conservation of Antarctic Seals of 1972. No formal animal ethics committee existed at the University of Pretoria in 1975. Data were gathered by observation with minimal disturbance to the fur seals during censuses and observation periods, and as such no ethical concerns are linked to the data gathering process.

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