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ARTICLE

Contest competition and injury in adult male sub-Antarctic fur seals

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Abstract

We recorded intra-sexual behaviour of adult male sub-Antarctic fur seals *Arctocephalus tropicalis* at Gough Island, Southern Ocean, during the 1975/76 summer breeding season. Our re-analysed data address male 'contest competition', which relates to the costs of intra-sexual disputes, including fights. We considered the risks/benefits of fighting through investigation of injuries ($n=353$) sustained by adult males ($n=124$) in fights. Injuries were predominantly on the forequarters, especially around the insertion areas of the front flippers (41%) with its sparse pelage, compared to the neck and chest areas combined (29%), an area which is well protected by thick pelage. The infliction of serious, sometimes debilitating, injuries to competitors increases a male's access to females. Injuries predominate in injured, defeated males that gather at non-breeding sites, suggesting that injuries inflicted by dominant males were successful in excluding competing males from breeding sites.

Keywords Body areas · Breeding season · Fur seal · Otariidae · Pinnipedia · Physical injury · Reproductive success · Territory defence

Introduction

Sub-Antarctic fur seals (Otariidae: *Arctocephalus tropicalis* (Gray 1872; SAFS hereafter) breed on islands in the Southern Ocean (Hofmeyr and Bester 2018). We studied them on Gough Island (Bester 1987). SAFS are polygamous, colonial breeders with adult males defending territories during the austral summer on beaches where adult females gather, give birth and mate over a highly synchronised period of approximately 6 weeks (Bester 1981, 1995). Adult male numbers on land peak in December (Bester 1981), when males of several fur seal species engage in many highly ritualized aggressive interactions (Rand 1967; Peterson 1968; Stirling 1971; Miller 1975) which may include physical combat. Aggressive encounters between adult males occur from early November to early January (Bester 1981, 1990). High levels of testosterone are a proximate cause of such overt aggression in both *A. tropicalis* (Bester 1990) and long-nosed (New Zealand) fur seals, *A. forsteri* (Lesson 1828) (Negro et al. 2010).

Physical contest competition characterizes competition for mates in some male marine mammals, in which aggressive interactions limit the access of competing males to females. The outcomes of physical contests amongst many species of male fur seals are influenced by multiple factors. Intrinsic physical and physiological factors include body size, strength, endurance, and energy reserves; behavioural factors include experience, and fighting techniques (including in defence); and extrinsic factors include territorial status (resident or intruder), access to water on a territory, and the presence of females (Peterson 1968; Stirling 1970, 1971; Miller 1975, 2018; Bester 1977, 1982a, b; McCann 1980; Francis and Boness 1991; Franco-Trecu et al. 2014; Campagna 2018).

We analysed data collected in 1975 (Bester 1977) at Gough Island (GI hereafter) to investigate the costs of intrasexual disputes through injuries received in physical contests, including fights, by adult male SAFS. Costs and risks of territoriality in fur seals include the danger of suffering physical injury or even death as a direct or secondary consequence of fighting injuries (Miller 2018).

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Material and methods

Study area

Gough Island (40°19′ S, 9°57′ W), in the South Atlantic Ocean (Fig. 1), supports the world's largest population of SAFS (Hofmeyr and Bester 2018). Different locations on GI are variously used by SAFS as established breeding, breeding, non-breeding, and idle colony sites (defined in Bester 1982a). During the 1975/76 breeding season, we visited multiple beaches on the East Coast of GI (Fig. 1) to count fur seals and to investigate time budgets and activity patterns (Bester 1981; Bester and Rossouw 1994). At a mean interval of about 10 days from recording the first injured adult males, opportunistically, we counted injured males and noted details of their wounds (Bester 1981; Bester and Rossouw 1994).

Recording of sightings

We used criteria of Condy (1978) and Jones et al. (2019) to distinguish adult males: large body size and a dorsum that varies from almost black to grey with a conspicuous cream to yellow chest and throat, extending up on the level of the ear pinnae, around the eyes, and across the bridge of the nose. This clearly separates from the dark colouration of the head and crest of longer hairs which comes to a marked point between the eyes (Fig. 2). We examined the adult males by the naked eye or (if necessary) with 7 × 42 binoculars for the presence, number and location of recently sustained external injuries; we did not count scars (i.e., completely healed wounds). We included all instances where the skin appeared to be broken, ranging from small compromised, suppurating/not suppurating areas, to large open wounds with underlying fat and muscle exposed. We categorized injured areas of the body as: head and throat (HT), chest (C), insertion of front flipper (FF) areas (left- and right-front flipper sides combined), neck (N), and hindquarters with back and rump combined (BR; Fig. 2). We could not control for the angle (horizontal/elevation) at which an individual was viewed, nor for its posture at rest or during physical contests (postures are described by Stirling 1970, 1971; Miller 1971; Bester 1977; Bester and Rossouw 1994), e.g., positioning themselves chest to chest (S1), that would affect visibility of wounds if present. We could not account which parts of each animal were not visible during the attempt to score injuries at each encounter. We scored right and left sides separately for FF injuries to evaluate whether there was a lateralized bias in (a) the way in which we scored wounds on injured animals, and (b) the fighting technique of the animals. We use the terms 'injuries' and 'wounds' synonymously.

Statistical analyses

We computed summary statistics on 124 individuals with 1–10 wounds, and excluded one outlier, a single male with

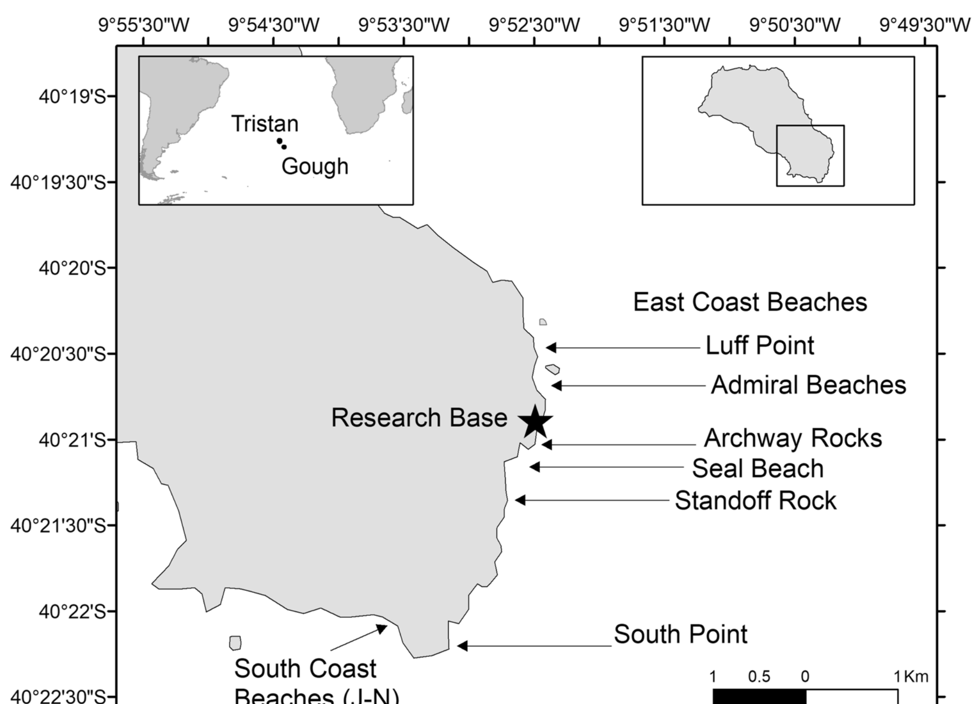

Fig. 1 Map of South Atlantic Ocean showing the location of GI, and the study locations on East Coast and South Coast beaches mentioned in the text

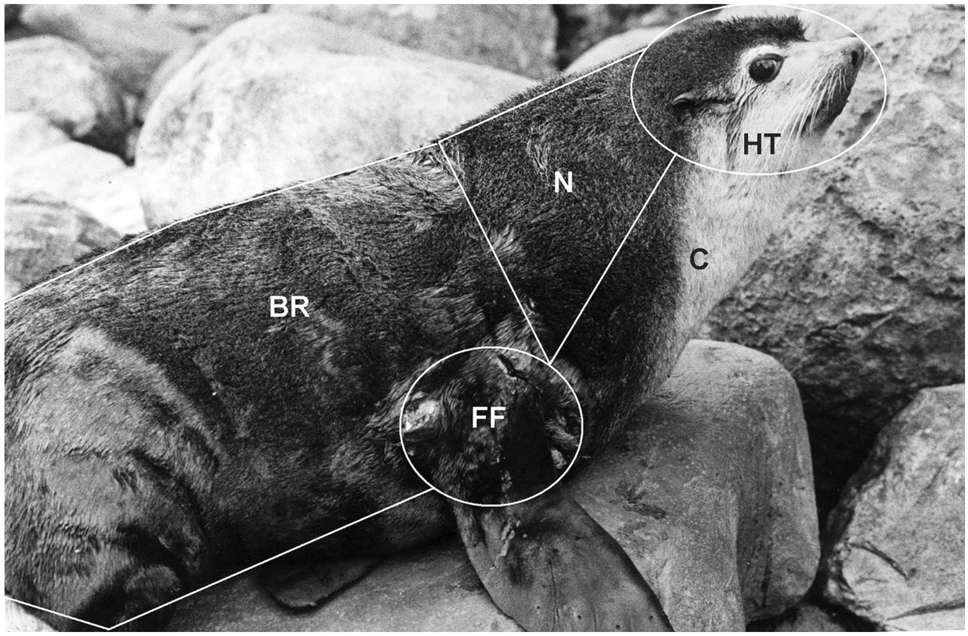

Fig. 2 Photograph of the right side of an injured SAFS male at GI with the various body areas indicated where wounds were recorded in this study. HT = head and throat; N = neck; C = chest; FF = insertion area of the front flipper; BR = back and rump combined. The overall total of wounds scored on both the right- and left side of each animal, fully or partially in view, were combined for each body area

17 wounds. This male likely received his wounds from multiple males simultaneously (see discussion).

We conducted statistical analyses with R version 4.3.1 (R Core Team 2023).

Results

Sightings and details about injured males are summarised in Tables 1 and 2. Most (ca. 60%) wounded adult males observed in December, during the peak in adult males ashore, were at Admiral North (Fig. 1). This relatively

Table 1 Number of wounds recorded for injured adult SAFS males at GI

Date	Locality	Number of injured males	Number of wounds for each area					Total number of wounds
			Head and throat	Chest	Front flipper areas	Neck	Back and rump	
1975/11/09	Admiral North	1	0	0	1	0	0	1
1975/11/09	Admiral Rest	2	0	0	4	0	0	4
1975/11/21	K Beach SC	3	2	0	5	0	0	7
1975/11/24	Admiral Rest	1	0	0	0	1	0	1
1975/11/24	Admiral North	7	2	3	8	0	0	13
1975/11/28	J Beach SC	2	0	0	1	3	0	4
1975/11/29	LN Beaches SC	4	2	0	9	4	2	17
1975/11/29	N Beach SC	5	7	0	4	0	0	11
1975/11/29	RN Beaches SC	7	5	1	8	5	2	21
1975/11/30	Admiral North	4	0	0	4	1	7	12
1975/12/06	MN Beaches SC	4	0	0	6	6	7	19
1975/12/11	Admiral North	27	4	6	37	17	31	95
1975/12/13	Seal Beach	13	0	2	14	13	7	36
1975/12/13	J Beach SC	7	2	4	1	6	3	16
1975/12/22	Tvl Bay Beaches	11	1	1	13	2	4	21
1975/12/27	Admiral North	26	2	10	30	17	16	75
	Total	124	27	27	145	75	79	353
	Percentage		7.6	7.6	41.1	21.2	22.4	

Table 2 Number of injured areas recorded for injured adult SAFS males at GI

Date	Locality	Number of injured males	Number of injured areas					Total number of injured areas
			Head and throat	Chest	Front flipper areas	Neck	Back and rump	
1975/11/09	Admiral North	1	0	0	1	0	0	1
1975/11/09	Admiral Rest	2	0	0	2	0	0	2
1975/11/21	K Beach SC	3	1	0	3	0	0	4
1975/11/24	Admiral Rest	1	0	0	0	1	0	1
1975/11/24	Admiral North	7	2	1	5	0	0	8
1975/11/28	J Beach SC	2	0	0	1	2	0	3
1975/11/29	LN Beaches SC	4	1	0	3	1	1	6
1975/11/29	N Beach SC	5	4	0	3	0	0	7
1975/11/29	RN Beaches SC	7	4	1	5	4	1	15
1975/11/30	Admiral North	4	0	0	2	1	4	7
1975/12/06	MN Beaches SC	4	0	0	3	4	3	10
1975/12/11	Admiral North	27	4	5	20	10	14	53
1975/12/13	Seal Beach	13	0	1	9	6	4	20
1975/12/13	J Beach SC	7	2	3	1	4	2	12
1975/12/22	Tvl Bay Beaches	11	1	1	9	2	3	16
1975/12/27	Admiral North	26	2	6	21	9	12	50
	Total	124	21	18	88	44	44	215
	Percentage		9.8	8.4	40.9	20.5	20.5	

small open boulder beach section held more than half of all wounded adult males scored over the entire research period (S2—Table 1). Other injuries were scored during traverses of the rest of the East Coast beaches, and the South Coast (J–N) beaches (Fig. 1). All wounded adult males were scored at a mean interval of 9.75 days ($n=10$, range 6–16 days) on the various stretches of coastline.

Overall, as tabulated in Table 1, injuries recorded ($n=353$) on adult males, were primarily scored on FF insertion areas combined, followed by the BR and N body areas. Both the FF insertion areas combined, cover a smaller surface area (see S1) than all other body part delineations, except for HT and C areas which sustained the fewest injuries. The number of individual injuries recorded on FF insertion areas on the left sides and on the right sides of males with FF insertion wounds (see S2—Table 2) did not differ significantly from each other ($\chi^2=0.0621$; $df=1$; p value $=0.8033$).

Both the number of injuries and the number of injured areas, scored per wounded adult male, were higher in December (2.98 wounds per male; 1.83 injured areas per male) than in November (2.53 wounds per male; 1.61 injured areas per male), respectively (S2—Table 2). The distribution of injuries ($n=353$ injuries) over the different body areas ($n=5$ areas) did not deviate significantly ($\chi^2=2.5823$; $df=4$; p value $=0.63$) from the distribution of injured areas ($n=215$ injured areas), where the number of injured areas were scored irrespective of the number of injuries to each area (i.e., any number of injuries scored on a particular area of an individual male counted as one). Similarly, the number of injured areas on the left sides and on the right sides of males with FF insertion wounds (see S2—Table 2) were not significantly different from each other ($\chi^2=0.0097$; $df=1$; p value $=0.9215$).

Discussion

Pinniped mating systems are classically characterized in terms of male competition and polygyny, but alternative male strategies and female choice also play a part (Hoffman et al. 2003). In the highly polygynous otariids, some male Juan Fernandez fur seals, *A. philippii,* uniquely amongst fur seals, hold completely aquatic territories (Francis and Boness 1991) while South American fur seals, *A. australis* (Franco-Trecu et al. 2014), and Northern fur seals, *C. ursinus* (Kiyota et al. 2008) include alternative male reproductive tactics as well. In Antarctic fur seals, *A. gazella*, female choice is an integral component of the mating system (Gemmell et al. 2001) but with no evidence of alternative male reproductive tactics such as aquatic or sneaky terrestrial mating (Hoffman et al. 2003).

Whether alternative male reproductive strategies improve male breeding success or not, holding a land-based territory confers varying advantage to male reproductive success (e.g., Francis and Boness 1991; Arnould and Duck 1997;

Gemmell et al. 2001). Territoriality and dominance hierarchies aim to improve the adult male's reproductive advantage (Stirling et al. 1993) which it clearly does in mid- and high latitude species in temperate and cold climates such as, e.g., the SAFS (this study), Antarctic fur seals (Arnould and Duck 1997) and Northern fur seals (Kiyota et al. 2008) where holding territories on land is the predominant male reproductive strategy.

Territorial boundary displays between fur seal males are largely ritualized, with outright fighting infrequent (Stirling 1971; McCann 1980; Miller 1971, 1975, 2018). The postural repertoires of fur seals include 'neck-waving' and 'oblique' displays which are used in conflict situations which precede actual physical contact between opposing adult males when a fight is imminent (Schusterman 1968; Stirling 1971; Miller 1971; Bester 1977; McCann 1980).

Fighting

Neck-waving typically involves males positioning themselves chest to chest (see S1), and they weave their heads and necks from side to side, usually out of phase with each other (Stirling 1970, 1971; Miller 1971; Bester 1977), presumably to gain an advantageous position from which to lunge and inflict a bite on the opponent. Most of the bites are directed anteriorly towards the face, chest and sides of the neck, followed/interspersed by quick lunges directed at the insertion of the front flippers (Bonner 1968; Bester 1977; McCann 1980; Campagna 2018). Lunges to the insertion of the front flippers are quick as these leave the back of the deliverer exposed to the opponent (Bonner 1968).

The record of visible injuries sustained to these and other areas of the male SAFS body results from the neck-waving fighting tactic, with most injuries ($n = 274$; 77.6%) sustained to the forequarters (head, throat, chest, neck, and fore-flipper areas). The remainder of the injuries (to the back and rump area) may be inflicted during fights (Stirling 1971) but are also inflicted on defeated, fleeing males and other male trespassers that are subjected to 'group aggression' by other territorial male fur seals (Paulian 1964; Rand 1967; Peterson 1968; Bonner 1968; Bester 1977; McCann 1980). Although these physical contacts that involve biting in territorial disputes only occur at 2.88% (Miller 1975), 5.0% (Gentry 1975), 8.39% (Bester 1977), and 14% (McCann 1980) of threat displays by adult male fur seals across territorial boundaries, the injuries sustained by adult males can be severe (Baker and McCann 1989).

Injuries

Injuries are sustained especially to the fore flippers or dorsal surface of the forequarters in fur seals (Miller 2018; this study). The chest and neck areas are protected by the males' heavy manes (Scheffer 1962; Bonner 1968; Stirling 1971; Condy and Green 1980; Mesnick and Ralls 2018) which renders injuries less conspicuous in these areas (Bonner 1968; Stirling 1971; this study), and many likely go undetected. Such effective protection rarely results in more than superficial wounds in Antarctic fur seals (Bonner 1968). Even after prolonged shaking and pulling, a bite to the neck area may not open a visible tear in the skin of *A. forsteri* (Stirling 1971).

On the other hand, the FF insertion area is a very vulnerable spot (McCann 1980) and has, by comparison to other dorsal body areas, a thin pelage (Bonner 1968). A sparse pelage loses partly its ability to protect a seal against mechanical injuries, the epidermis and dermis taking over that function (Sokolov 1960). Consequently, skin layers in naked flipper areas are thicker than layers in fur-covered areas of both *A. p. pusillus* (Rotherham et al. 2005) and SAFS (Bester and Van Ouwerkerk 2023) which protect them against abrasions in the absence of hair. However, the absence of a dense hair covering which improves evaporative thermoregulation in dorsal flipper regions (Rotherham et al. 2005; da Silva et al. 2020; Bester and Van Ouwerkerk 2023), leaves FF insertion areas especially prone to accumulate severe, conspicuous wounds sustained in fights between territorial males (this study). Such injury would conceivably shorten the duration of a physical contest between SAFS males (Bester 1977), with its accompanying advantages of lesser energy use and reduced thermal loading (Bester and Rossouw 1994).

The high prevalence of wounded adult males found (in December 1975) at the Admiral N idle colony (Plate 1a—Bester 1982a), results from this area holding almost exclusively adult males (Bester 1982a). These adult males represent injured individuals which unsuccessfully attempted to procure a territory at a breeding colony site, or were evicted from one; males in prime physical condition apparently not bold or strong enough to compete; and old males (Bester 1982a).

The period of territory establishment in November, especially towards the end of the month when there is an influx of large males that replaced resident adult males (Bester 1977), results in territory changes through fighting (Miller 1975; Bester 1977; Campagna 2018). This contrasts with the period of territory maintenance in December when territorial disputes are rarely settled through infliction of wounds (Gentry 1975; Miller 1975; Bester 1977; McCann 1980).

During the peak breeding season in December 1975, the calculated median birthdate was 13 December (Bester 1987), and mothers come into oestrus and mate within 8–12 h following parturition (Hofmeyr and Bester 2018). Access to large numbers of mothers in oestrus at this time is expected to promote aggressive interactions, and the sustaining of injuries during fighting amongst territorial males. Further, injuries sustained during the earlier period of territory establishment when the rate of encounters is higher than in the period thereafter in *A. p. pusillus* (Rand 1967), *A. forsteri* (Stirling 1971), and *A. gazella* (McCann 1980) would still be visible at this later stage and thereafter. Severe (entanglement) injuries to *A. forsteri* took months or even years to fully close (Boren et al. 2006) and we suggest that even lesser injuries caused by fighting are expected to remain for a number of weeks at least, which would allow their inclusion in this survey.

Outcomes

Male–male behaviour must be correlated with copulation frequency whenever possible (Stirling et al. 1993) if territoriality and dominance hierarchies are to improve the adult male's reproductive advantage. Clearly, this was not possible to determine for SAFS (present study) which hold territories on land as is typical of fur seals. However, the adult male tactic to inflict serious, sometimes debilitating injury to the vulnerable FF insertion areas of opponents, is likely to secure a positive outcome in male territory defence, and, therefore, access to females. A quick, lasting, positive outcome would also satisfy the dual advantages of limiting endogenous heat production and likely heat stress (during lengthy contests), and energy conservation to prolong the presence of successful seals at the breeding colony and increase their reproductive potential (Stirling 1971; Bester and Rossouw 1994). The preponderance of such injuries inflicted to the FF insertion areas of the males found on idle colony sites where injured, defeated bulls gather (Bester 1982a), suggests that such injuries to opponents have the desired effects (of eliminating the opposition and, therefore, gaining reproductive advantage) in the short (breeding season) term. The high mortality rate in Antarctic fur seal males on the breeding beaches of Bird Island, South Georgia, was mainly caused by infections of fighting wounds and pneumonias (Baker and McCann 1989). Such fighting injuries were especially to the fore flippers or dorsal surface of the forequarters (Miller 2018).

The similarity in number of individual injuries ($n = 145$) recorded on FF insertion areas on the left sides ($n = 74$) and right sides ($n = 71$) of all individuals with FF insertion wounds ($n = 88$) has a twofold interpretation. It may suggest that (a) the two sides of animals were visible to observers at equal rates for scoring FF insertion injuries, and/or that (b) individual males' fighting techniques did not show lateralized behaviour (see Pryaslova et al. 2009), as wounds were inflicted on combatants' FF insertion areas (left vs. right) in equal measure.

The similarity between the number of wounds sustained in each of the five body areas (with FF areas combined), and the number of times any particular body area received at least one wound, calculated for each individual ($n = 124$), suggests that the vulnerability ranking (most to least) for the delineated body areas is correct. The vulnerability ranking, using injured area rather than number of wounds on it, buffers against the number of wounds that may have gone unnoticed due to the differences in pelage protection of the different areas of the body. It also dampens the influence of sustaining more than one wound to a specific area as a result of a single interaction between competing males (i.e., overstating one interaction's importance in accruing injury), compared to injury inflicted during more than one, separate interactions between contestants.

Caveats

It is likely that many injuries sustained by adult male fur seals go undetected by observers, especially in the chest and neck areas, which have ample pelage protection. Also, not all individuals present themselves so that all areas of the body are visible on any particular occasion for the scoring of injuries. Frequently, only the right or left side of an individual is visible, side on or obliquely, or only the front quarters as compared to the hind quarters. It is also not known whether the same animal had been sighted, and recorded, more than once, or even that such an animal(s) presented the same or different sides/postures on subsequent sighting(s).

However, the time lapses of approximately 10 days between visits to particular areas visited more than once, the seasonal (Bester 1981) and especially the large daily (Bester and Rossouw 1994) flux in numbers of adult males ashore, suggest that such repeated sightings are likely to be few. Male fur seals are not rigidly tied to territories and territorial behaviour, and may change locations (Carey 1991; Miller 2018) such as during times of excessive heat loading (Francis and Boness 1991; Bester and Rossouw 1994) which also influences the selection of beaches for haulout (Bester 1982b). Furthermore, to minimize repeated sightings, a number of territorial males ($n = 43$), as far as we could identify them individually on external morphological characteristics alone, were only scored once for wounds, in the peak breeding season from 6 to 13 December in 1975. These males held area-specific territories, which we controlled for delineation of borders (and, therefore, the extent of use by the territorial males). This allowed eventual calculation of territory sizes on particular beaches (Bester 1977) which we followed more or less closely.

Conclusions

Aspects other than inflicting wounds on adversaries also determine the outcome of territorial disputes amongst adult males. However, the record of visible injuries sustained to the various areas of the adult male *A. tropicalis* body during disputes suggests that the FF insertion areas are preferentially targeted to overcome opponents in physical fights that involve biting. We suggest that either one or the other of the two sides of an animal were equally presented to observers owing to similar rates for scoring FF insertion injuries. Also, the similarity in absolute number of injuries, and the area-specific injuries irrespective of numbers of injuries sustained, to left and right FF insertion areas, discounts the possible influence of lateralized behaviour. The care taken to minimize counting wounds on the same individuals more than once by (a) staggering the occasions to record injuries by about 10 days, and (b) recording males occupying known territories only once during the peak of the breeding season, may have been sufficient in limiting re-recordings. Additionally, the seasonal and daily fluctuation in numbers of adult males ashore would promote the scoring of injuries on different individuals on the various occasions. The vulnerability ranking of body areas that sustained injury, by counting injured areas as opposed to the number of wounds sustained in the various areas, would buffer against the influence of unnoticed wounds. It would also prevent overstating the importance of any single encounters which inflicted numerous wounds. A quick, lasting, positive outcome to territorial dispute consequent on significant injury to vulnerable FF insertion areas of opponents, would likely promote the dual advantages to the inflictor of reducing endogenous heat production and heat stress (that otherwise would be generated during lengthy contests), and energy conservation. Such outcomes would prolong the adult male sub-Antarctic fur seals' presence at the breeding colony and increase their reproductive potential.

There is a need for descriptive (including quantitative) comparative studies to document the frequency, distribution, nature, and pathology of injuries received in pinniped combat, using standardized descriptions and reporting. This information is needed for interpreting theoretical, conceptual, and modelling approaches about combat behaviour in the group.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10164-024-00811-x.

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Author contributions MNB planned the study, and together with GJR, recorded all the observations. MNB drafted the manuscript and is responsible for the photographs. MNB and GJR sourced relevant scientific literature and PJvS performed the statistical analyses. MNB and PJvS read, edited, and approved the final manuscript.

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Data availability All data generated and analysed during this study are included in this published article and its supplementary information files.

Declarations

Conflict of interest We declare that we have no conflict of interest.

Ethical approval Field procedures in 1975 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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