Natal site fidelity by breeding female southern elephant seals in relation to their history of participation in the winter haulout

4 authors:

Greg Hofmeyr
Port Elizabeth Museum
87 PUBLICATIONS   1,857 CITATIONS

Stephen Kirkman
Oceans and Coasts
147 PUBLICATIONS   4,222 CITATIONS

Pierre A. Pistorius
Nelson Mandela University
229 PUBLICATIONS   4,156 CITATIONS

Marthán N. Bester
University of Pretoria
513 PUBLICATIONS   9,299 CITATIONS

African Journal of Marine Science

Natal site fidelity by breeding female southern elephant seals in relation to their history of participation in the winter haulout

GJG Hofmeyr [a b] , SP Kirkman [a c d] , PA Pistorius [a e] & MN Bester [a]

[a] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, Pretoria, 0028, South Africa

[b] Port Elizabeth Museum at Bayworld, PO Box 13147, Humewood, 6013, South Africa

[c] Oceans and Coasts, Department of Environmental Affairs, Private Bag X2, Rogge Bay, 8012, South Africa

[d] Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch, 7701, South Africa

[e] Department of Zoology, Nelson Mandela Metropolitan University, South Campus, PO Box 77000, Port Elizabeth, 6031, South Africa

PLEASE SCROLL DOWN FOR ARTICLE

Natal site fidelity by breeding female southern elephant seals in relation to their history of participation in the winter haulout

GJG Hofmeyr[1,2]*, SP Kirkman[1,3], PA Pistorius[1,4] and MN Bester[1]

[1] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa

[2] Current address: Port Elizabeth Museum at Bayworld, PO Box 13147, Humewood 6013, South Africa

[3] Current address: Oceans and Coasts, Department of Environmental Affairs, Private Bag X2, Rogge Bay 8012, South Africa, and Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, South Africa

[4] Current address: Department of Zoology, Nelson Mandela Metropolitan University, South Campus, PO Box 77000, Port Elizabeth 6031, South Africa

* Corresponding author, e-mail: greg@bayworld.co.za

Of the four types of terrestrial haulout periods undertaken by southern elephant seals *Mirounga leonina*, only the purpose of the winter haulout is unknown. Returning to a haulout site from distant pelagic foraging grounds bears significant costs in terms of increased energy expenditure, reduced foraging time and increased exposure to predation; therefore, each haulout must serve a purpose. We examined the hypothesis that the winter haulout serves to maintain familiarity with the natal site, thereby increasing site fidelity. To this end, we analysed a long-term mark-recapture dataset for female southern elephant seals at Marion Island, Southern Ocean. Results indicate that, whereas greater natal site fidelity as primiparous females was associated with recorded presence ashore at the study site during the winter haulout as immatures, this was not the case for multiparous females. Furthermore, recorded presence ashore during both the moult haulouts as immatures, and all haulouts as immatures, irrespective of haulout type, was also associated with increased site fidelity. This suggests that any haulout at the natal island as an immature seal, whether for the moult or winter haulout, assists in maintaining site fidelity. Therefore, while the winter haulout facilitates greater natal site fidelity, whether this is the sole reason for this terrestrial period remains uncertain.

Keywords: animal movement, dispersal, *Mirounga leonina*, Subantarctic

Introduction

Southern elephant seals *Mirounga leonina* are the largest of all pinnipeds, with some adult males reaching three tonnes (Laws 1993). They inhabit the waters of the Southern Ocean, spending some 70–85% of their lives at sea (Carrick et al. 1962a, McIntyre et al. 2010). They undertake a highly synchronised biannual migration between pelagic foraging grounds and haulout sites on isolated Subantarctic islands (Carrick et al. 1962a, Hindell and Burton 1988, Bester and Pansegrouw 1992, Jonker and Bester 1998). Southern elephant seals are ashore for four types of protracted terrestrial periods during the course of their lives: (1) during the natal period, pups will spend 2–3 months ashore after birth and prior to going to sea for the first time; (2) all southern elephant seals participate in the annual moult haulout of approximately a month (excluding pups of the year, which moult at three weeks of age); (3) the majority of adults will participate in an annual breeding haulout; and (4) the winter haulout (Laws 1956, Carrick et al. 1962a, Hindell and Burton 1988, Wilkinson 1992, Le Boeuf and Laws 1994). The winter haulout, also termed the resting haulout, mid-year haulout or autumn-winter haulout (Carrick et al. 1962a, Burton 1985, Wilkinson 1992, Wheatley 2001), is undertaken during the austral autumn and winter, predominantly by immature

animals (Laws 1956, Carrick et al. 1962a, Condy 1979, Hindell and Burton 1988, Kirkman et al. 2001).

Returning to a terrestrial haulout site bears significant costs. Elephant seal foraging areas and haulout sites are usually far apart, typically a few hundred or thousand kilometres and seals must therefore expend much time and energy migrating between sites (Hindell and Burton 1988, Bester and Pansegrouw 1992, Jonker and Bester 1998, Field et al. 2001, Biuw et al. 2007, Tosh et al. 2009, Bailleul et al. 2010, McIntyre et al. 2011). Further costs are incurred due to the fast that accompanies a terrestrial haulout (Slip et al. 1992, Wheatley 2001). Moreover, southern elephant seals are subject to an increased risk of predation by killer whales *Orcinus orca* at haulout sites (Condy et al. 1978, Ridoux 1986, Guinet 1991, Keith et al. 2001, Pistorius et al. 2002a, Tosh et al. 2008, Reisinger et al. 2011). The annual timing of visits by killer whales to Subantarctic islands coincides with periods of increased elephant seal activity in the vicinity of these islands (Condy et al. 1978, Keith et al. 2001). While sightings of these killer whales are most common during the elephant seal breeding season from September to December of each year, a second but smaller peak occurs in March–May when underyearling and other

elephant seals return to terrestrial habitat for their winter haulout (Voisin 1972, Condy et al. 1978, Guinet 1991, Keith et al. 2001).

Despite the costs, elephant seals have no choice but to be ashore during certain periods. They are born ashore and spend the first few weeks of life ashore (Laws 1956, Carrick et al. 1962a, Lenglart and Bester 1982, Wilkinson and Bester 1990), and must be ashore to moult. During this phase, the entire outer layer of skin and all hair is lost and thermoregulatory abilities are compromised (Slip et al. 1992, Worthy et al. 1992, Boyd et al. 1993), rendering this haulout obligatory. Although there is substantial evidence that some mating does take place at sea, most is thought to take place during the breeding haulout (de Bruyn et al. 2011).

Whereas all other terrestrial periods are obligatory, it is not known whether this is the case for the winter haulout. Individual animals may come ashore between one and three times per year during the winter, but some are thought to skip participation in this type of haulout in any given year (Carrick et al. 1962a, Wilkinson 1992, Kirkman et al. 2001). Despite the apparently optional nature of the winter haulout, considering the investment in time and energy, and the predation risks, the winter haulout must have a purpose. A number of possibilities have been suggested (many reviewed in Burton 1985), one of which is that repeated visits ensure greater familiarity to the natal island and therefore allow greater site fidelity during breeding haulouts as an adult (Burton 1985, Pistorius et al. 2002b). Pistorius et al. (2002b) found significantly higher resighting rates at the island of their birth for seals that had been recorded ashore during the winter haulout compared to those that had not.

Site fidelity in migratory animals has been shown for a number of species and is thought to be beneficial for a variety of reasons (Greenwood 1980, Bateson 1982, Shields 1987, Pusey and Wolf 1996). Elephant seals also show site fidelity (Carrick and Ingham 1962a, Nichols 1970, Campagna and Lewis 1992, Hofmeyr 2000), possibly because their own survival indicates that their natal site is a suitable breeding site (Hofmeyr 2000). Furthermore, familiarity with a site may aid seals in securing and retaining the resources required during the breeding haulout (Hofmeyr 2000). It is also possible that their return to the vicinity of a previously used site may aid them in selecting habitat suitable for raising a pup to weaning.

In this study we examined the possibility that the winter haulout serves to increase site fidelity by examining the effect that the history of participation in the winter haulout has on fidelity to individual beaches at the location of the study, Marion Island, during the breeding season. We also compared this to the history of resights of individuals during moult haulouts undertaken as immatures.

Marion Island in the Southern Ocean (46°54′ S, 37°45′ E) supports a population of approximately 2 100 elephant seals with some 500 pups born annually (Pistorius et al. 2004; Mammal Research Institute, unpublished data). A long-term mark-recapture programme has yielded considerable data on the Marion Island elephant seal population. We used these data to examine the influence of the history of participation in the winter haulout by immature females on their later fidelity to natal sites during the breeding haulouts. Given that multiparous adult female elephant seals show significant

fidelity to the site of the first breeding event (Hofmeyr 2000), we assessed the site fidelity of primiparous and multiparous females separately. We attempted to answer the following questions: what portion of breeding animals are recorded ashore as immatures during various haulout events; is a history of participation at the natal island in the winter haulout as immature animals associated with increased fidelity to their natal site by incipient (primiparous) breeding adult females; and is the history of participation in the winter haulout as immature animals associated with fidelity of those hauling out during subsequent breeding seasons (multiparous animals)? To determine whether any relationship found between site fidelity and recorded presence ashore during the winter haulout was unique, we further investigated whether the history of resights during moult haulouts when immature was associated with natal site fidelity by both primiparous and multiparous breeding females, and whether the history of resights during all haulouts when immature, irrespective of type, was associated with natal site fidelity by both primiparous and multiparous breeding females.

Material and methods

Study site
Marion Island is in one of two islands in the Prince Edward Islands archipelago. Southern elephant seals regularly haul out on 41 beaches on the north-east and east coasts, and part of south coast of the island (Figure 1). Irregular searches elsewhere indicate that very few seals come ashore outside of this area (Mulaudzi et al. 2008). All but two of the beaches on Marion Island are separated from neighbouring beaches by cliffs or other terrain that is generally impassable to elephant seals. Seals are required to swim between most sites and the sites can therefore be regarded as distinct entities. Distances between sites were measured on a map as the shortest distance along the coastline from the centre of one site to another. Indentations along the coastline were ignored.

Field work
From 1983, all elephant seals born on Marion Island were marked within days of weaning at their natal site, with known exceptions in two years, estimated at 2% and 5% of those cohorts. All seals were tagged with Jumbo Rototags (Dalton, Henley-on-Thames, England) in the interdigital webbing of each of their hind-flippers. A unique combination of tag colours and numbers allowed for subsequent recognition of individuals.

In association with the above, a resight programme was also initiated in 1983. This comprised systematic searches for seals ashore within the study area. Searches were conducted approximately weekly during the annual breeding haulout (August–November) and every 10 days at other times of the year. Up to 1990, searches of the north-east and east coast took place from September to May with monthly searches of the south coast. From 1990, these beaches were visited throughout the year, following the same pattern, and since September 1992 the southern beaches were also visited every 7 or 10 days. During these searches the haulout site, haulout type, moult status (if moulting) and breeding status (if breeding) of tagged seals
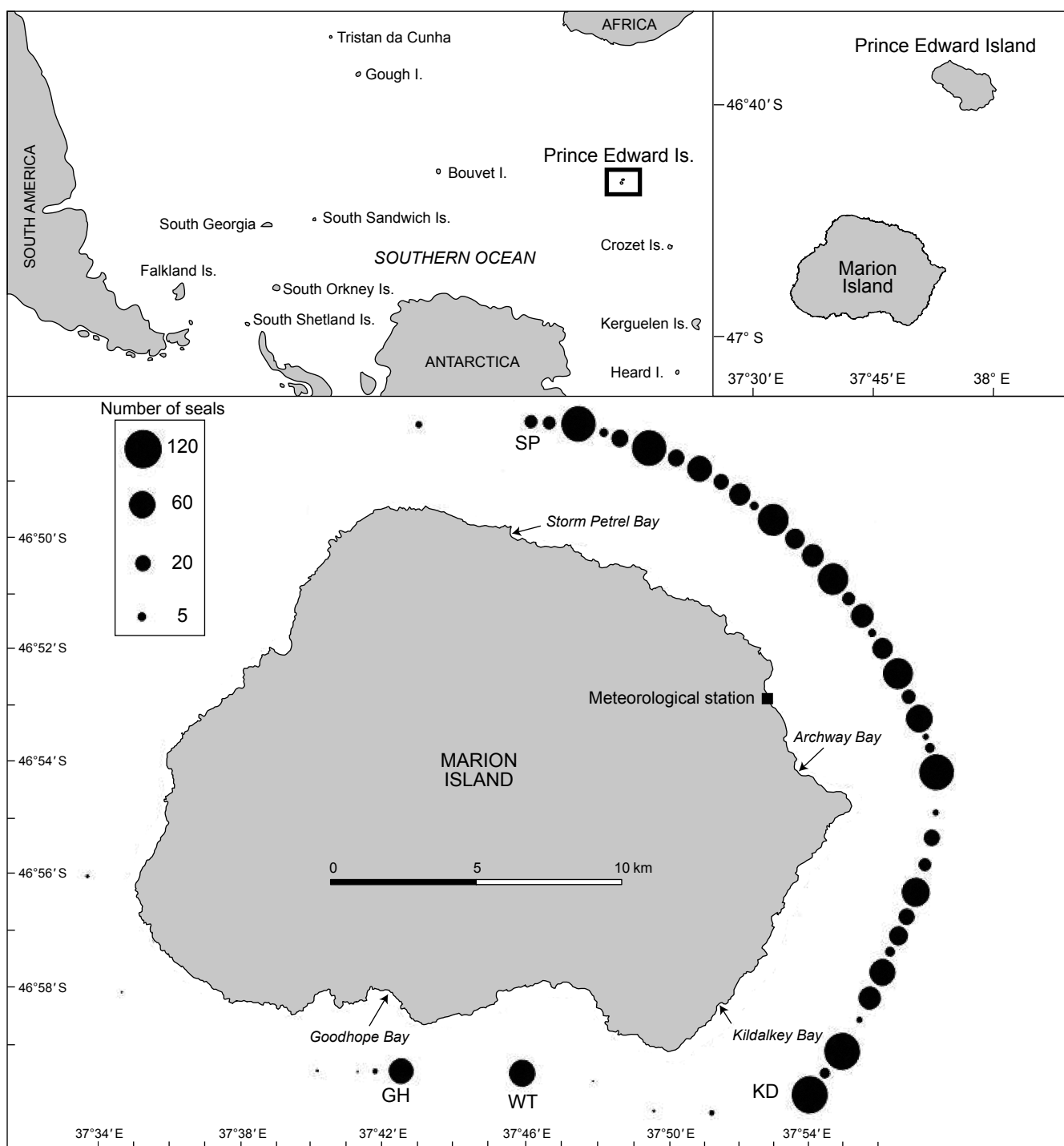
Figure 1: Map of Marion Island showing the distribution of southern elephant seals *Mirounga leonina*. The areas of the circles are directly proportional to the mean annual number of elephant seals hauling out at each site. The north and east sections of the coastline between locations marked SP and KD and at locations marked WT and GH form the study area

were recorded, together with the identifying tag colour and number. Seals were assumed to age by one year on the peak haulout date of the breeding season (15 October) in each year, following Wilkinson (1992). Animals that had hauled out for the breeding season before the 15 October, however, were assumed to age by a year at the start of their breeding haulout.

Data editing and analysis

The database comprised 78 218 records of tagging and resighting seals during the period November 1983–December 2003. Prior to analysis, this database was edited in three stages:

(1) Records of animals whose sex was never identified were removed. In addition, records with obvious errors

were either corrected or removed if they could not be corrected. These corrections reduced the database to 70 538 records;

(2) Each individual seal was potentially recorded multiple times during a single breeding event. To facilitate analysis, replicate records for each haulout event were discarded; single records were selected to be representative of each breeding haulout in each year by each seal. The selected records were either (i) the first record at the location where she was sighted most often with a pup, (ii) if she was not sighted with a pup, then the first record of the location where she was sighted most often, or (iii) where she was not sighted with a pup and the number of records at different locations were equal, then the first record of the first location. The resulting database consisted of 34 082 records;

(3) Immature animals are defined as those younger than three years of age (Laws 1956, Carrick et al. 1962a).

A number of animals may not be observed during haulouts if they have lost both tags, have been missed by observers or have hauled out elsewhere (see Pistorius et al. 2004 for a discussion of resighting probabilities). Therefore, only those females recorded ashore for the first time between the ages of 3–6 years inclusive were classified as primiparous. Records of females recorded breeding for the first time at ages older than six years were assumed to have bred elsewhere first and were thus discarded. Only 2.7% of females recorded surviving to breed were recorded to breed for the first time seven years or older (Mammal Research Institute, unpublished data). Once a female was recorded ashore for a second breeding season, irrespective of age, she was classified as multiparous.

Effects of the history of participation in winter or moult haulouts by immatures on natal site fidelity by breeding animals was assessed using two methods: by comparing frequency distributions of the distances from natal to breeding sites between animals that had and had not participated in specific haulout events; and comparing the frequency distributions of the distances from natal to breeding sites between categories of animals that were defined by the number of years that they had participated in a specific haulout type. Data were analysed using standard non-parametric tests: the Kruskal-Wallis ANOVA, with multiple comparison of ranks *post hoc* tests where significance was found, and the Kolmogorov-Smirnov test. Significance was set at $p < 0.05$.

Results

Participation in winter and moult haulouts by immature animals at the study site

The proportions of breeding female southern elephant seals recorded ashore at Marion Island when immature varied with age. Whereas between 70% and 80% had been observed to haul out in winter or to moult as yearlings at the study site, or to moult as two-year-olds, only approximately half had been observed in winter as underyearlings and one third to winter as two-year-olds (Figure 2). Approximately 85% of adult females hauling out to breed as adults did so at least once at the study site during a winter while immature, but only 13% were observed to haul out in all winter haulouts

during their first three years of life (Figure 3a). Over 85% of breeding adult females were recorded to moult at least once at the study site as an immature animal (Figure 3b). Only approximately half of the breeding adult females had been recorded during the moult at the study site as both yearlings and two-year-olds. A total of 96% of breeding female southern elephant seals had been recorded ashore at least once during a winter or moult haulout as an immature, but only 9% of breeding females had been recorded ashore during all haulouts as an immature (Figure 3c).

Natal site fidelity and history of winter haulout participation of primiparous females

Females that had participated in winter haulouts at Marion Island as underyearlings (Kolmogorov-Smirnov, $n_1 = 501$, $n_2 = 626$, $p < 0.025$), as yearlings (Kolmogorov-Smirnov, $n_1 = 761$, $n_2 = 365$, $p < 0.005$) or as two-year-olds (Kolmogorov-Smirnov, $n_1 = 350$, $n_2 = 777$, $p < 0.025$) hauled out significantly closer to their natal sites during their first breeding season than females that had not (Figure 4). Furthermore, the number of winter haulouts participated in to the age of three had a significant effect on fidelity to natal site during first breeding haulout (Kruskal-Wallis ANOVA: $H_{(3,1126)} = 22.5$, $p < 0.001$). *Post hoc* tests indicated that this difference lay entirely between those that had not hauled out at the study site during a winter as an immature animal and those that had hauled out once ($z = 3.2$, $p = 0.010$), twice ($z = 4.5$, $p < 0.001$) or three times previously ($z = 3.6$, $p < 0.002$) (Figure 5).

Natal site fidelity and history of winter haulout participation of multiparous females

Although breeding multiparous females that had been recorded as juveniles during winter haulouts showed higher natal site fidelity than those that were not (Figure 6), these differences were not significant whether the comparison was of their history as underyearlings (Kolmogorov-Smirnov, $n_1 = 840$, $n_2 = 937$, $p > 0.10$), yearlings (Kolmogorov-Smirnov, $n_1 = 1\,248$, $n_2 = 529$, $p > 0.10$) or two-year-olds (Kolmogorov-Smirnov, $n_1 = 569$, $n_2 = 1\,208$, $p > 0.10$). In addition, the number of winter haulouts participated in as an
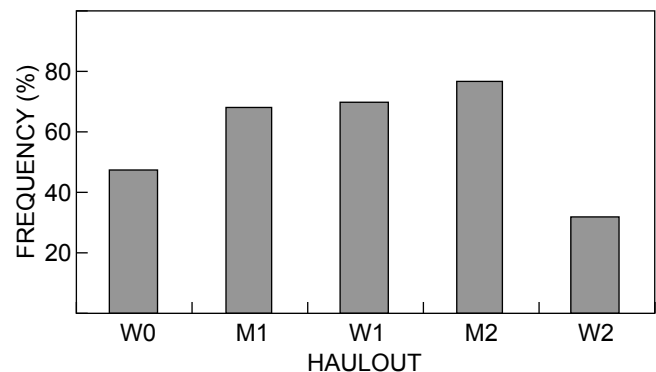
Figure 2: Percentage of breeding female southern elephant seals that were recorded ashore on Marion Island as immature animals during three possible winter haulouts (W0 — as underyearling, W1 — as a yearling, W2 — as two-year-old) and two possible moult haulouts (M1 — as a yearling, M2 — as a two-year-old)

immature animal had no significant influence (Kruskal-Wallis ANOVA: $H_{(3,1777)}$ = 1.89, p = 0.60) on fidelity to natal site of females hauling out to breed in years subsequent to their first breeding haulout (Figure 7).

Natal site fidelity and history of moult haulout participation of primiparous females

The record of tagged seals ashore during specific moult seasons (Figure 8) indicates that those that had hauled out to moult at the study site as yearlings bred closer to their natal site than those that had not, although not significantly so (Kolmogorov-Smirnov, n_1 = 760, n_2 = 367, p > 0.10). Those that had hauled out to moult as two-year-olds, however, did breed significantly closer to their natal site than those that had not done so (Kolmogorov-Smirnov, n_1 = 805, n_2 = 322, p < 0.01). The number of moult haulouts during which individuals had been observed in the study site while immature (Figure 9) had a significant influence on fidelity to natal site of breeding primiparous females (Kruskal-
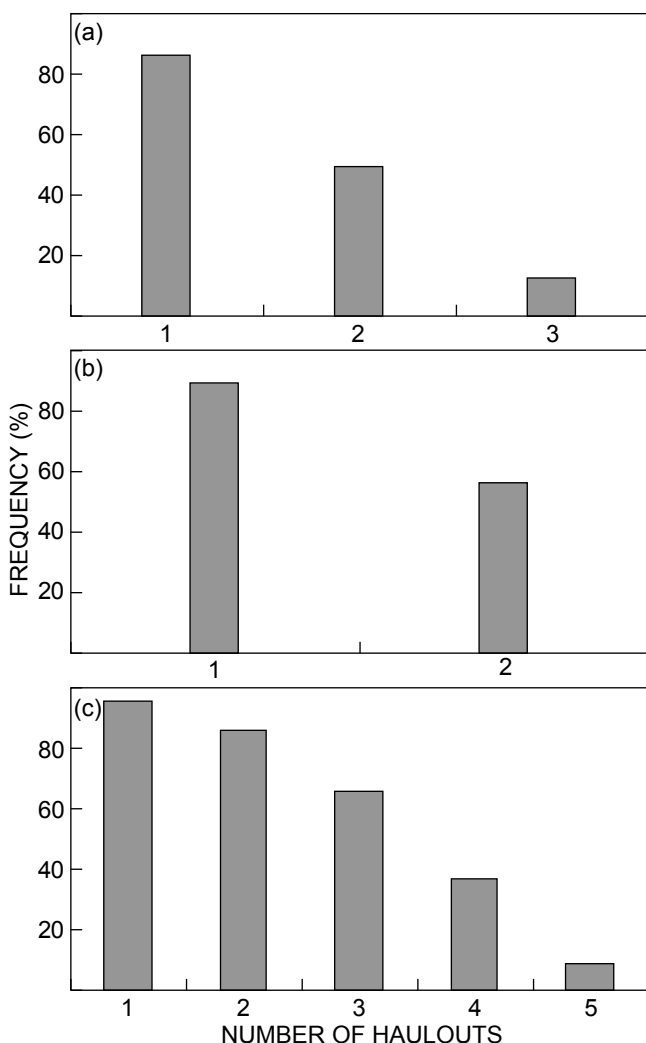
Wallis ANOVA: $H_{(3,1127)}$ = 17.38, p < 0.001). *Post hoc* tests indicated that females that had hauled out at least once (z = 3.43, p < 0.002) or twice (z = 4.12, p < 0.001) at the study site as an immature animal, bred significantly closer to their natal site the first time they hauled out to breed than those that had not hauled out at all.

Natal site fidelity and history of moult haulout participation of multiparous females

Multiparous female elephant seals that had moulted at the study site as yearlings bred significantly closer to their
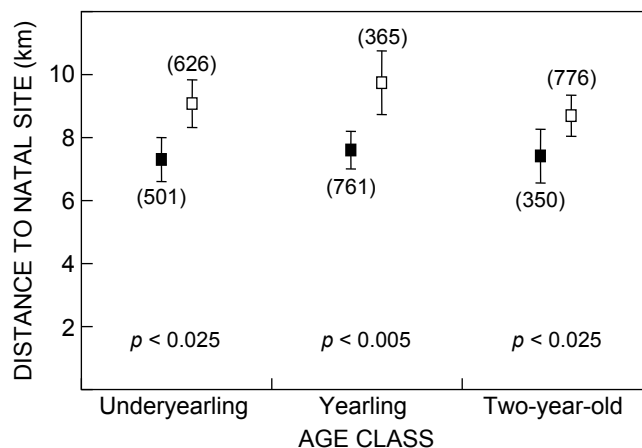

Figure 3: Percentage of all breeding female southern elephant seals recorded ashore as immature animals at Marion Island during (a) one, two or all three winter haulouts, (b) one or both moult haulouts and (c) at least one, two, three, four or in all five haulouts

Figure 4: Mean distance (± 95% confidence limits) between natal and breeding site of primiparous female southern elephant seals in relation to their history of presence or absence during specific winter haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, whereas open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The probability of significance (p) is shown (Kolmagorov-Smirnov test)
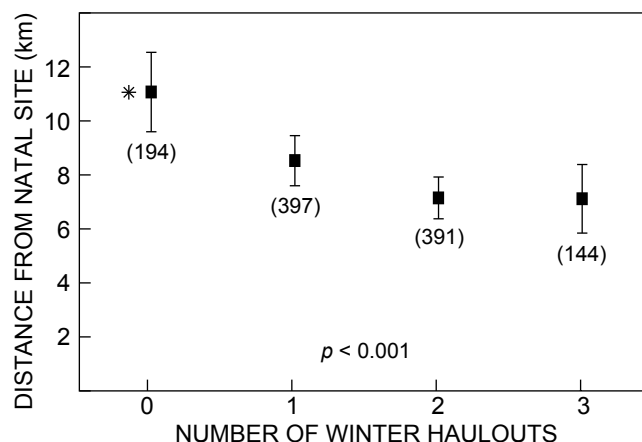

Figure 5: Mean distance (± 95% confidence limits) between the natal and breeding sites of primiparous female southern elephant seals, grouped following the number of winter haulouts recorded ashore at Marion Island when immatures. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others (Kruskal-Wallis ANOVA)
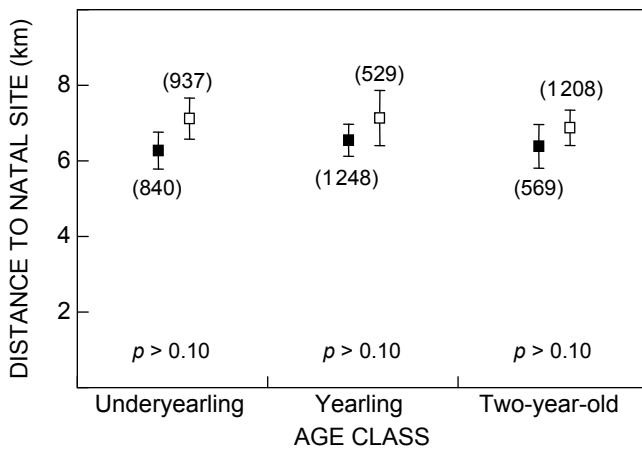
Figure 6: Mean distance (± 95% confidence limits) between natal and breeding site of multiparous female southern elephant seals in relation to their history of presence or absence during specific winter haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, while open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The probability of significance (*p*) is shown (Kolmagorov-Smirnov test)
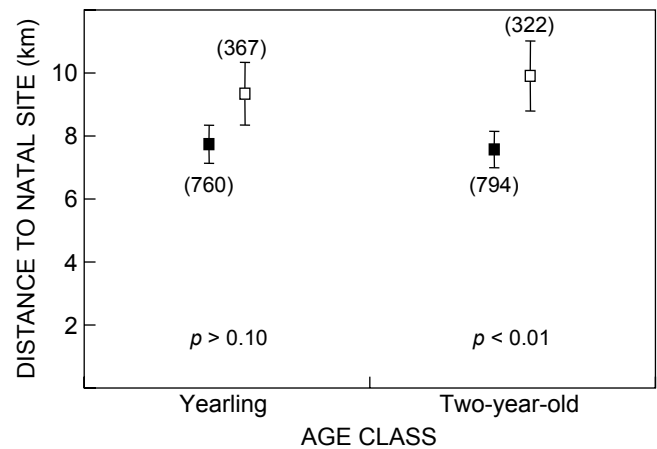

Figure 8: Mean distance (± 95% confidence limits) between natal and breeding site of primiparous female southern elephant seals in relation to their history of presence or absence during specific moult haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, while open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The probability of significance (*p*) is shown (Kolmagorov-Smirnov test)
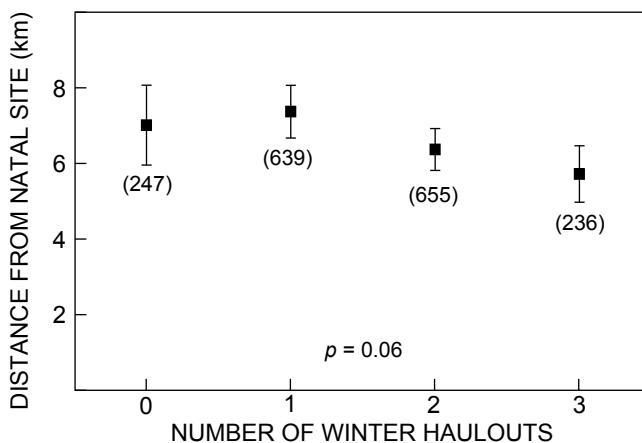

Figure 7: Mean distance (± 95% confidence limits) between the natal and breeding sites of multiparous female southern elephant seals, grouped following the number of winter haulouts recorded ashore at Marion Island when immatures. Numbers in parentheses are sample sizes. The probability of significance (*p*) is shown (Kruskal-Wallis ANOVA)
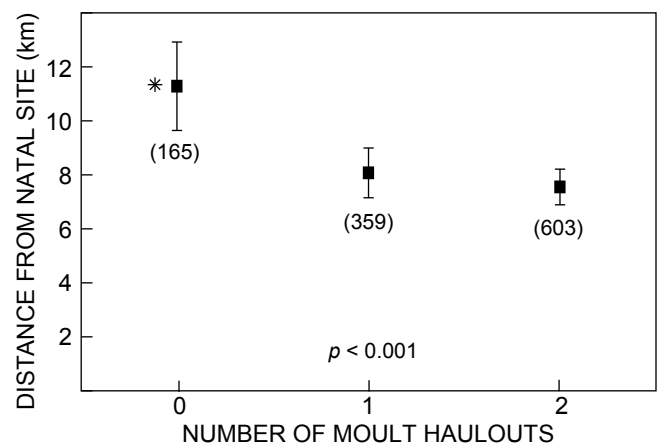

Figure 9: Mean distance (± 95% confidence limits) between the natal and breeding sites of primiparous female southern elephant seals, grouped following the number of moult haulouts recorded ashore at Marion Island when immatures. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others. The probability of significance (*p*) is shown (Kruskal-Wallis ANOVA)

natal site than those that had not done so (Kolmogorov-Smirnov, $n_1 = 1\,207$, $n_2 = 570$, $p < 0.001$) (Figure 10). Similarly, those that moulted at the study site as two-year-olds also bred significantly closer to their natal site (Kolmogorov-Smirnov, $n_1 = 1\,367$, $n_2 = 410$, $p < 0.025$). The number of moult haulouts that seals were recorded to participate in as immature animals (Figure 11) also had a significant effect on the fidelity to natal site when breeding (Kruskal-Wallis ANOVA: $H_{(2,1777)} = 15.59$, $p < 0.001$). Multiparous seals that had been recorded to moult twice at the study site as immature animals, hauled out significantly

closer to their natal site to breed than those that had not been recorded ($z = 3.41$, $p = 0.002$) or recorded once only ($z = 2.75$, $p = 0.018$).

Natal site fidelity and history of participation in all haulouts of primiparous females

The fidelity to natal site by adult females hauling out to breed for the first time was significantly related to the number of times they were recorded present during all haulouts when immature (Kruskal-Wallis ANOVA: $H_{(5,1127)} =$
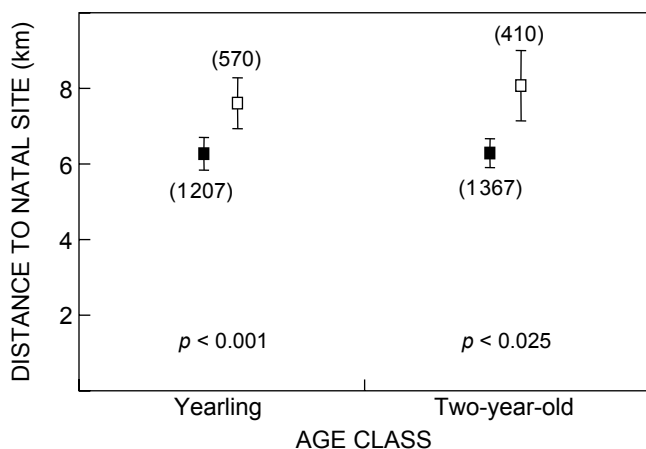
Figure 10: Mean distance (± 95% confidence limits) between natal and breeding site of multiparous female southern elephant seals in relation to their history of presence or absence during specific moult haulouts at Marion Island. The age class indicated is that at which the previous haulout took place. Closed squares indicate animals that were recorded ashore during a specific event, while open squares indicate animals that were not recorded ashore during that event. Numbers in parentheses are sample sizes. The significance level is shown (Kolmagorov-Smirnov test)
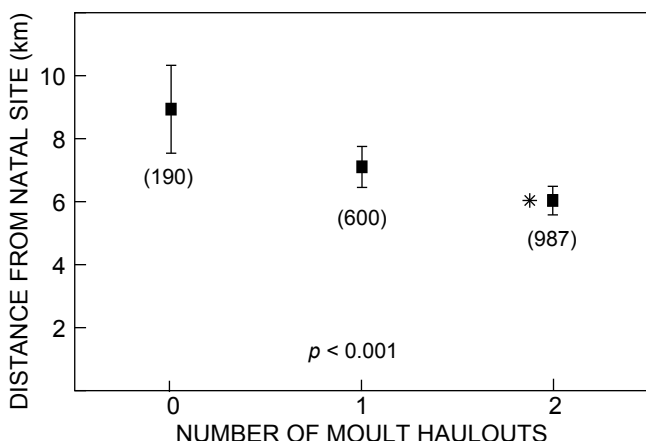

Figure 11: Mean distance (± 95% confidence limits) between the natal and breeding sites of multiparous female southern elephant seals, grouped following the number of moult haulouts recorded ashore at Marion Island when immatures. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others. The significance level is shown (Kruskal-Wallis ANOVA)

Figure 12: Mean distance (± 95% confidence limits) between the natal and breeding sites of primiparous female southern elephant seals, grouped following the number of haulouts recorded ashore at Marion Island when immatures. Numbers in parentheses are sample sizes. An asterisk marks the group that is significantly different from all others, except group 1. The significance level is shown (Kruskal-Wallis ANOVA)

Figure 13: Mean distance (± 95% confidence limits) between the natal and breeding sites of multiparous female southern elephant seals, grouped following the number of haulouts recorded ashore at Marion Island when immatures. Numbers in parentheses are sample sizes. The significance level is shown (Kruskal-Wallis ANOVA)

Natal site fidelity and history of participation in all haulouts of multiparous females

Presence or absence during haulouts as immature animals had no significant influence on later fidelity to natal site by multiparous breeding females (Kruskal-Wallis ANOVA: $H_{(5,1777)} = 10.49$, $p = 0.06$). Nonetheless, individuals that hauled out as immatures tended to haul out closer to their natal sites to breed (Figure 13).

Discussion

Conducting the first intensive study of a group of marked southern elephant seals, Carrick et al. (1962a, p 149) stated that 'The adaptive significance of virtual detachment from

33.81, $p < 0.001$) (Figure 12). Multiple comparisons *post hoc* tests revealed a significant difference between those that were not recorded to haul out between birth and the first breeding haulout, and those that were recorded to haul out twice ($z = 4.46$, $p = 0.001$), three times ($z = 4.06$, $p = 0.001$), four times ($z = 5.13$, $p = 0.001$) and five times ($z = 4.17$, $p = 0.001$). There was also a significant difference between those hauling out once and those hauling out four times ($z = 3.01$, $p < 0.05$). All other *post hoc* tests were not significant.
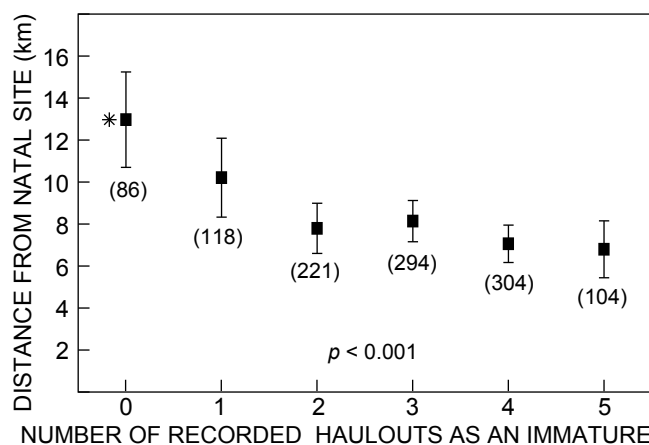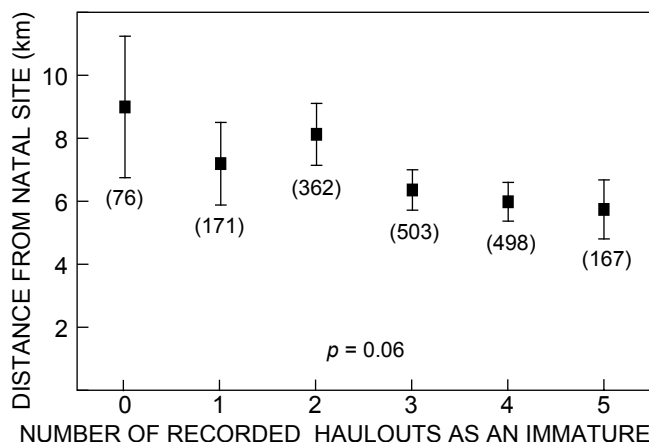
the sea during breeding and moulting is fairly obvious, but the autumn-winter haul-out presents a puzzle'. The function of this haulout remains a puzzle (Burton 1985, Pistorius et al. 2002b), perhaps because it is perceived as the least important of the terrestrial phases undertaken by this species and as such has been the least examined. A number of suggestions concerning its function have been made (many reviewed in Burton 1985): the winter haulout is a resting haulout (Carrick et al. 1962a, Panagis 1981, Bester 1989, Ling and Bryden 1992), allowing animals to conserve energy (Burton 1985); it allows immature animals to digest food (Mathews 1952 cited in Carrick et al. 1962b); it allows the strengthening of dentine to take place (Carrick et al. 1962a, Carrick and Ingham 1962b); it is a training period for terrestrial activities and allows physiological conditioning of the body to later terrestrial periods (Carrick et al. 1962a); it allows immature animals to avoid competing with adults for food resources (Burton 1985); and repeated visits ensure greater familiarity to the natal island and therefore allow greater site fidelity during breeding haulouts as an adult (Burton 1985, Pistorius et al. 2002b). Whereas this last hypothesis is the major focus of our paper, evidence for the other suggestions are briefly discussed.

Of the abovementioned hypotheses, the most widely accepted is that the winter haulout allows the animals to rest. Resting implies conserving energy, but when considering the amount of energy that would be required to cover the vast distances between foraging locations and terrestrial haulouts (Hindell and Burton 1988, Bester and Pansegrouw 1992, Jonker and Bester 1998, Field et al. 2001, Biuw et al. 2007, Tosh et al. 2009, Bailleul et al. 2010), this hypothesis seems implausible. It is possible, however, that those animals feeding in the vicinity of haulout site during the winter come ashore to rest. In support of the winter haulout as a possible resting haulout, Wheatley (2001) noted that immature female elephant seals with a lower weaning mass were more likely to be recorded ashore during the winter. Possibly these animals were unable to sustain long periods at sea.

Related to the above is the hypothesis that young animals come ashore to digest food. Pinnipeds, including southern elephant seals, however, have digestive rates of less than 24 hours (Markussen 1993, Krockenberger and Bryden 1994). Therefore, the duration of a winter haulout of several weeks is much longer than is necessary. Furthermore, as Carrick et al. (1962a) have noted, it is implausible that much digestion will take place on land due to the substantial distances between foraging locations and the haulout site. Whereas elephant seals of different age classes show differences in foraging behaviour (Lewis et al. 2006, McIntyre et al. 2010), and it is therefore possible that immatures feed closer to Marion Island than adults, immature elephant seals hauling out at Macquarie Island fed at sites distant from that island (van den Hoff et al. 2002, Field et al. 2005).

Carrick and Ingham (1962b) suggested that the winter haulout allows the hardening of dentine. They noted that the physiological demands of continual deep diving on immature animals may affect the growth of teeth, especially as the dive response reduces a number of physiological activities. This may be particularly important for males, as they grow larger teeth than females. They also mature later than females (Laws 1956) and participate in winter haulouts

for more years than females (Kirkman et al. 2001). Whereas the hardening of dentine theory is plausible, many elephant seals are thought not to haul out during the winter (Kirkman et al. 2001). A related suggestion is that the winter haulout is a physiological conditioning period (Carrick et al. 1962a, Burton 1985). It is possible that the physiological demands of the moult haulout (Slip et al. 1992, Worthy et al. 1992, Boyd et al. 1993) inhibit the required levels of conditioning during such haulouts. Wheatley (2001), however, noted no difference in at-sea mass gain, moult mass loss rate or body composition of immatures during the moult whether they were recorded ashore during the previous winter or not.

Burton (1985) suggested that by hauling out during the winter, immature animals avoid competition with adults. During this time, adults of both sexes feed in preparation for the energetically taxing breeding season (Reiter 1991, Boyd et al. 1994, Arnbom et al. 1997). The winter is therefore likely to be a particularly competitive foraging period. Significant competition between animals of various ages and age–sex classes is indicated by some separation in foraging areas (Bornemann et al. 2000, McConnell et al. 2002, Field et al. 2004, 2005) and differences in diet (Field et al. 2007).

Pistorius et al. (2002b) suggested that the winter haulout may serve to increase site fidelity of southern elephant seals by facilitating familiarity with the natal island. In support of this, they found that the probability of resighting animals at their natal island increased if they had been present during at least one winter haulout when immature. Our results support their findings for primiparous but not for multiparous females. We have further shown that the relationship between winter haulouts and natal site fidelity is evident not only for the natal island, as demonstrated by Pistorius et al. (2002b), but also at a finer hierarchical level, to that of individual natal beaches. We also found, however, that greater fidelity was linked not only to recorded presence during winter haulouts as immature animals, but also to their presence during moult haulouts as immature animals, and in fact to their presence during all haulouts of immature animals at the study site. Moreover, we found that, whereas natal site fidelity by multiparous females was not linked to their recorded presence ashore during winter haulouts, it is significantly linked to recorded presence ashore during moult haulouts when immature.

The implications of these findings are that, whereas participation in the winter haulout may facilitate greater familiarity with the natal site, this might not be the sole reason, or even a reason at all, for the existence of the winter haulout, considering that presence ashore during the moult haulout also facilitates greater natal site fidelity. In fact, the results indicate that, while site fidelity of primiparous females is increased by at least one visit to the natal island as an immature, further visits and the type of visit may not be important in terms of increasing site fidelity. The purpose of the winter haulout thus remains unknown.

The lack of an association between natal site fidelity of multiparous breeding females and their recorded presence or absence during winter haulouts is possibly due to the greater duration of the period since these visits. Hofmeyr (2000) found that younger primiparous females at Marion Island showed greater natal site fidelity than older primiparous females. While it is not known which navigational cues

are used by seals to locate a haulout site, it is possible that memories of a previously visited site fade with time.

Of the female elephant seals born on Marion Island and later recorded to breed there, some 30% were not recorded moulting at the study site as yearlings, and 20% were not recorded moulting as two-year-olds. Given that an annual moult haulout is thought to be obligatory (Slip et al. 1992, Worthy et al. 1992, Boyd et al. 1993), it is likely that the absent animals moulted elsewhere. Bester and Hofmeyr (2005) and Oosthuizen et al. (2009) recorded tagged immature elephant seals moulting on neighbouring Prince Edward Island, whereas Bester (1989) recorded seals tagged on Marion Island moulting as immature animals on Île de la Possession in the Crozet Archipelago, some 900 km away, and immature seals tagged on Île de la Possession, moulting on Marion Island. These percentages of animals not recorded during the moult are similar to the percentages of these age classes not recorded during the winter haulout at the study site by yearlings. Although the winter haulout has been considered to be optional (Carrick et al. 1962a, Wilkinson 1992, Kirkman et al. 2001), it is possible (as immature animals must moult elsewhere when they are not recorded at the study site) that immature animals also do not miss a winter haulout either, at least not as underyearlings and yearlings, hauling out on neighbouring or more distant islands when they are not recorded on their natal island. To further address the questions posed by the winter haulout, some idea of the levels of participation in this haulout is required. Fitting a suitable sample of immature animals with satellite tags of sufficient battery duration prior to their first pelagic phase and at the end of annual moults should provide valuable data in this regard.

References

Arnbom T, Fedak MA, Boyd IL. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology* 471–483.

Bailleul F, Cotté C, Guinet C. 2010. Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Marine Ecology Progress Series* 408: 251–264.

Bateson PPG. 1982. Preference for cousins in Japanese quail. *Nature* 295: 236–237.

Bester MN. 1989. Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Marine Mammal Science* 5: 257–265.

Bester MN, Pansegrouw HM. 1992. Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science* 88: 574–575.

Bester MN, Hofmeyr GJG. 2005. Numbers of elephant seals at Prince Edward Island, Southern Ocean. *South African Journal of Wildlife Research* 35: 85–88.

Biuw M, Boehme L, Guinet C, Hindell MA, Costa D, Charrassin J-B, Roquet F, Bailleul F, Meredith M, Thorpe S, Tremblay Y, McDonald B, Park Y-H, Rintoul SR, Bindoff N, Goebel M, Crocker D, Lovell P, Nicholson J, Monks F, Fedak MA. 2007. Variation in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proceedings of the National Academy of Sciences* 104: 13705–13710.

Bornemann H, Kreyscher M, Ramdohr S, Martin T, Carlini A, Sellmann L, Plötz J. 2000. Southern elephant seal movements and Antarctic sea ice. *Antarctic Science* 12: 3–15.

Boyd IL, Arnbom T, Fedak MA. 1993. Water flux, body composition and metabolic rate during molt in female southern elephant seals (*Mirounga leonina*). *Physiological Zoology* 66: 43–60.

Boyd IL, Arnbom TA, Fedak MA. 1994. Biomass and energy consumption of the South Georgia population of southern elephant seals. In: Le Boeuf BJ, Laws RM (eds), *Elephant seals: population ecology, behavior and physiology.* Berkeley: University of California Press. pp 98–120.

Burton HR. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In: Ling JK, Bryden MM (eds), *Studies of sea mammals in south latitudes.* South Australia: Geographic Services (Pty) Ltd. pp 19–30.

Campagna C, Lewis M. 1992. Growth and distribution of a southern elephant seal colony. *Marine Mammal Science* 8: 387–396.

Carrick R, Csordas SE, Ingham SE. 1962b. Studies of the southern elephant seal *Mirounga leonina* (L.). IV Breeding and development. *CSIRO Wildlife Research* 7: 161–197.

Carrick R, Csordas SE, Ingham SE, Keith K. 1962a. Studies of the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *CSIRO Wildlife Research* 7: 119–160.

Carrick R, Ingham SE. 1962a. Studies on the southern elephant seal, *Mirounga leonina* (L.) V. Population dynamics and utilization. *CSIRO Wildlife Research* 7: 198–206.

Carrick R, Ingham SE. 1962b. Studies on the southern elephant seal *Mirounga leonina* (L.). II. Canine tooth structure in relation to function and age determination. *CSIRO Wildlife Research* 7: 102–118.

Condy PR. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Zoology* 14: 95–102.

Condy PR, van Aarde RJ, Bester MN. 1978. The seasonal occurrence and behaviour of killer whales *Orcinus orca*, at Marion Island. *Journal of Zoology* 184: 449–464.

de Bruyn PJN, Tosh CA, Bester MN, Cameron EZ, McIntyre T, Wilkinson IS. 2011. Sex at sea: alternative mating system in an extremely polygynous mammal. *Animal Behaviour* 82: 445–451.

Field IC, Bradshaw CJA, Burton HR, Hindell MA. 2004. Seasonal use of oceanographic and fisheries management zones by juvenile southern elephant seals (*Mirounga leonina*) from Macquarie Island. *Polar Biology* 27: 432–440.

Field IC, Bradshaw CJA, Burton HR, Sumner MD, Hindell MA. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Oecologia* 142: 127–135.

Field IC, Bradshaw CJA, van den Hoff J, Burton HR, Hindell MA. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology* 150: 1441–1452.

Field I[C], Hindell M, Slip D, Michael K. 2001. Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science* 13: 371–379.

Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140–1162.

Guinet C. 1991. L'orque (*Orcinus orca*) authour de l'archipel Crozet

comparaison avec d'autres localites. *Revue d'Ecologie (la Terre et la Vie)* 46: 321–337.

Hindell MA, Burton HR. 1988. The history of the elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. *Papers and Proceedings of the Royal Society of Tasmania* 122: 159–168.

Hofmeyr GJG. 2000. Dispersal and dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. MSc thesis, University of Pretoria, South Africa.

Jonker FC, Bester MN. 1998. Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarctic Science* 10: 21–30.

Keith M, Bester MN, Bartlett PA, Baker D. 2001. Killer whales (*Orcinus orca*) at Marion Island, Southern Ocean. *African Zoology* 36: 163–175.

Kirkman SP, Bester MN, Pistorius PA, Hofmeyr GJG, Owen R, Mecenero S. 2001. Participation in the winter haulout by southern elephant seals (*Mirounga leonina*). *Antarctic Science* 13: 380–384.

Krockenberger MB, Bryden MM. 1994. Rate of passage of digesta through the alimentary tract of southern elephant seals (*Mirounga leonina*) (Carnivora: Phocidae). *Journal of Zoology* 234: 229–237.

Laws RM. 1956. The elephant seal (*Mirounga leonina* Linn.). II. General social and reproductive behaviour. *Falkland Islands Dependencies Survey Scientific Reports* 13: 1–88.

Laws RM. 1993. Identification of species. In: Laws RM (eds), *Antarctic seals: research methods and techniques.* Cambridge: Cambridge University Press. pp 1–28.

Le Boeuf BJ, Laws RM. 1994. Elephant seals: an introduction to the genus. In: Le Boeuf BJ, Laws RM (eds), *Elephant seals: population ecology, behavior and physiology.* Berkeley: University of California Press. pp 1–26.

Lenglart PY, Bester MN. 1982. Post-weaning dispersion of southern elephant seal *Mirounga leonina* underyearlings at Kerguelen. *Revue d'Ecologie (la Terre at la Vie)* 36: 175–186.

Lewis R, O'Connell TC, Lewis M, Campagna C, Hoelzel AR. 2006. Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*). *Proceedings of the Royal Society, Series B* 273: 2901–2907.

Ling JK, Bryden MM. 1992. *Mirounga leonina*. *Mammalian Species* 391: 1–8.

Markussen NH. 1993. Transit time of digesta in captive harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology* 71: 1071–1073.

McConnell B, Fedak MA, Burton HR, Engelhard GH. 2002. Foraging areas of naïve recently weaned southern elephant seal pups. *Journal of Animal Ecology* 71: 65–78.

McIntyre T, Bornemann H, Plötz J, Tosh CA, Bester MN. 2011. Water column use and forage strategies of female southern elephant seals from Marion Island. *Marine Biology* 158: 2125–2139.

McIntyre T, de Bruyn PJN, Ansorge IJ, Bester MN, Bornemann H, Plötz J, Tosh CA. 2010. A lifetime at depth: vertical distribution of southern elephant seals in the water column. *Polar Biology* 33: 1037–1048.

Mulaudzi TW, Hofmeyr GJG, Bester MN, Kirkman SP, Pistorius PA, Jonker FC, Makhado AB, Owen JH, Grimbeek RJ. 2008. Haulout site selection of southern elephant seals at Marion Island. *African Zoology* 43: 25–33.

Nichols DG. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.), of Macquarie Island. *Mammalia* 34: 598–616.

Oosthuizen WC, Bester MN, de Bruyn PJN, Hofmeyr GJG. 2009. Intra-archipelago moult dispersion of southern elephant seals at the Prince Edward Islands, southern Indian Ocean. *African*

Journal of Marine Science 31: 457–462.

Panagis K. 1981. Local movement of southern elephant seal pups *Mirounga leonina* (Linn.) at Marion Island. *South African Journal of Antarctic Research* 10/11: 28–31.

Pistorius PA, Bester MN, Lewis MN, Taylor FE, Campagna C, Kirkman SP. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). *Journal of Zoology* 263: 107–119.

Pistorius PA, Kirkman SP, Bester MN, Taylor FE. 2002b. Implications of the winter haulout for future survival and resighting probability of southern elephant seals at Marion Island. *South African Journal of Wildlife Research* 32: 59–63.

Pistorius PA, Taylor FE, Louw C, Hanise B, Bester MN, de Wet C, du Plooy A, Green N, Klasen N, Podile S, Schoeman J. 2002a. Distribution, movement, and estimated population size of killer whales at Marion Island, December 2000. *South African Journal of Wildlife Research* 32: 1–7.

Pusey AE, Wolf M. 1996. Inbreeding avoidance in animals. *Trends in Ecology and Evolution* 11: 201–206.

Reisinger RR, de Bruyn PJN, Bester MN. 2011. Predatory impact of killer whales on pinniped and penguin populations at the Subantarctic Prince Edward Islands: fact and fiction. *Journal of Zoology* 285: 1–10.

Reiter J. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. *Behavioral Ecology and Sociobiology* 28: 153–160.

Ridoux V. 1986. Feeding association between seabirds and killer whales, *Orcinus orca*, around subantarctic Crozet Islands. *Canadian Journal of Zoology* 65: 2113–2115.

Shields WM. 1987. Dispersal and mating systems: investigating their causal connections. In: Chepko-Sade BD, Halpin ZT (eds), *Mammalian dispersal patterns: the effects of social structure on population genetics.* Chicago: University of Chicago Press. pp 3–24.

Slip DJ, Gales NJ, Burton HR. 1992. Body-mass loss, utilization of blubber and fat, and energetic requirements of male southern elephant seals, *Mirounga leonina*, during the molting fast. *Australian Journal of Zoology* 40: 235–243.

Tosh CA, Bornemann H, Ramdohr S, Schröder M, Martin T, Carlini A, Plötz J, Bester MN. 2009. Adult male southern elephant seals from King George Island utilize the Weddell Sea. *Antarctic Science* 21: 113–121.

Tosh CA, de Bruyn PJN, Bester MN. 2008. Preliminary analysis of the social structure of killer whales, *Orcinus orca*, at subantarctic Marion Island. *Marine Mammal Science* 24: 929–940.

Van den Hoff J, Burton HR, Hindell MA, Sumner MD, McMahon CR. 2002. Migrations and foraging of juvenile southern elephant seals from Macquarie Island within CCAMLR managed areas. *Antarctic Science* 14: 134–145.

Voisin J-F. 1972. Notes on the behaviour of the killer whale, *Orcinus orca* (L.). *Norwegian Journal of Zoology* 20: 93–96.

Wheatley KE. 2001. Behavioural and physiological aspects of the mid-year haul-out for southern elephant seals (*Mirounga leonina*) on Macquarie Island. MPhil thesis, St Andrews University, UK.

Wilkinson IS. 1992. Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. PhD thesis, University of Pretoria, South Africa.

Wilkinson IS, Bester MN. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *Journal of Zoology* 222: 591–600.

Worthy GAJ, Morris PA, Costa DP, Le Boeuf BJ. 1992. Moult energetics of the northern elephant seal (*Mirounga angustirostris*). *Journal of Zoology* 227: 257–265.