Intra-archipelago moult dispersion of southern elephant seals at the Prince Edward Islands, southern Indian Ocean

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Manuscript received June 2009; accepted September 2009

During three summer surveys at Prince Edward Island (PEI), southern Indian Ocean (2001, 2004 and 2008), 416 southern elephant seals *Mirounga leonina* were inspected for identification tags. In all, 42 seals that had been tagged as weaned pups at their natal site were found on Marion Island (MI), 38 of which could be individually identified by resighting their tag numbers. The majority of the MI-tagged seals were yearlings or subadults, and all but one were hauled out at PEI for the annual moult. The attendance rate of the known individuals at their natal island during the annual moult was only 40%, based on their resighting histories. This was significantly lower than the 77 ± 6% moult attendance rate estimated for a random MI population sample drawn from the same cohorts (based on 10 000 replications). Annual resight probabilities (considering all haulout phases) was 58% per annum for the MI seals seen at PEI, and 80 ± 4% for the simulation. Seasonal and annual absences of seals from MI violate the 'homogeneity of capture' assumption of mark–recapture models. When multiple sightings during any year are treated as a single sighting, resights during other haulouts (e.g. breeding) compensate only partially for absences during the moult. Therefore, mark–recapture studies undertaken in archipelagos should ideally include both marking and resighting of individuals on all islands which will allow discrimination between mortality and local migration.

Keywords: capture heterogeneity, dispersal, mark–resight, *Mirounga leonina*, movement, Prince Edward Islands, site fidelity, sub-Antarctic

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Introduction

The Prince Edward Islands (PEIs) in the sub-Antarctic region of the southern Indian Ocean (Figure 1) comprise two islands, Marion Island (MI; 290 km²) and Prince Edward Island (PEI; 46 km²). The PEIs constitute an isolated surface feature within this region of the Southern Ocean and large populations of seabirds and three species of seals use the terrestrial habitat as breeding and moulting sites (Ryan and Bester 2008). The archipelago's southern elephant seal *Mirounga leonina* population is relatively small (c. 520 and 130 pups born annually on MI and PEI respectively; Bester and Hofmeyr 2005, Mammal Research Institute, unpublished data) and forms part of the larger Kerguelen 'stock', along with the Crozet and Kerguelen island groups and Heard Island (Figure 1) (Laws 1994). Southern elephant seals haul out onto both MI and PEI — usually returning to the vicinity of their natal beaches (Hofmeyr 2000) to rest (chiefly immature seals), breed (adults) and moult (annual obligatory haulout for all the seals) (Kirkman et al. 2001, 2003, 2004).

Each year at MI since 1983, all or nearly all of the weaned elephant seal pups of each birth cohort have been tagged for future identification, by fieldworkers stationed at the island. To resight these marked animals, most of the beaches utilised by elephant seals at MI have been frequented every 7–10 days throughout this long-term study. In contrast, mark–resight effort at PEI has been extremely low: only a portion of a single elephant seal cohort has been tagged (in 2004) and resightings of tagged animals have only occurred on 13 days over the past 15 years. The reason for this is that visits to PEI are restricted, to protect its relatively pristine environment (PEIMPWG 1996). The operative inaccessibility of PEI potentially results in an observational 'sink area' for tagged MI-seals (seals alive and present at the PEIs, but not resighted) in sharp contrast to the detectability of marked seals at MI, which approaches 100%. Although it is assumed that emigration of southern elephant seals from MI has a negligible influence on modelling of population parameters for this population (e.g. Pistorius et al. 1999), some elephant seals marked at MI have been recorded resting at PEI, 19 km distant and the only other island in the PEI archipelago, during autumn–winter (Bester 1989). Even if such displacement is temporary, it could have implications for the MI mark–resight study: if some individuals temporarily disperse from MI while others are perpetually available for resighting,

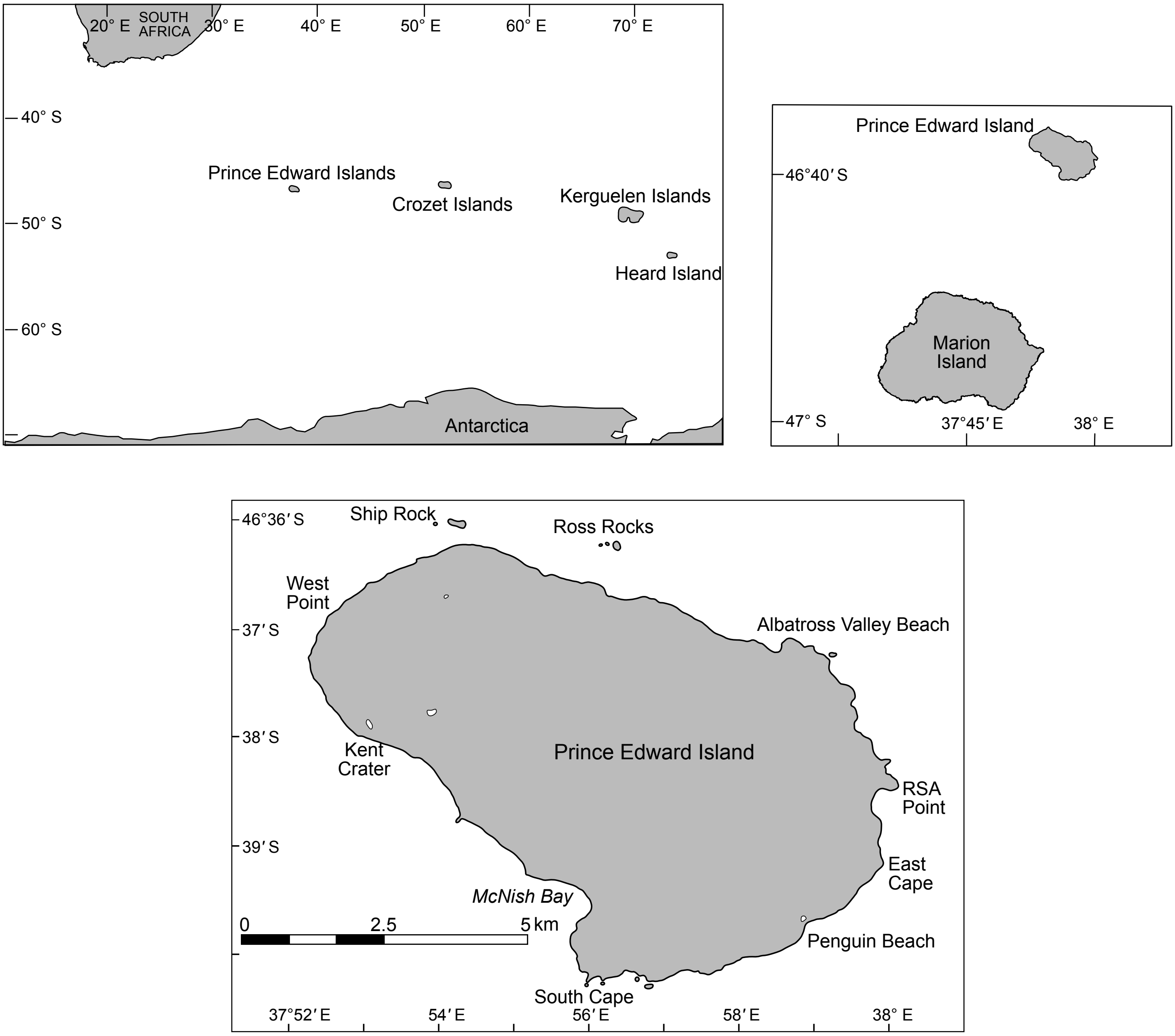

Figure 1: Maps showing the position of the Prince Edward Island group in the southern Indian Ocean, the two islands within the archipelago, and the elephant seal survey areas on Prince Edward Island

heterogeneous capture probabilities would result in violation of mark–resight model assumptions.

Survey expeditions to PEI in the summers of 2001, 2004 and 2008 allowed us to investigate movements of tagged elephant seals between MI and PEI during the season of the moult, to investigate the possible effects of observed movements for the ongoing mark–resight programme at MI. More specifically, the aims of this study were:

1. to investigate intra-archipelago movements of elephant seals in the PEI group, including resights of MI-tagged seals during three summer surveys on PEI, and resights of seals tagged at PEI in 2004 at MI;
2. to determine whether or not the resighting histories of MI-tagged seals observed at PEI are typical for individuals of the MI population, by assessing the frequency of haulouts at MI throughout their recorded life histories;
3. to discuss the significance of the findings for the ongoing mark–resight programme at MI.

Material and methods

MI mark–recapture protocol

Recently weaned elephant seal pups have been double-tagged annually at MI from 1983 to 2008 (total 12 370, range 389–700 per year) with uniquely numbered, colour-coded plastic Dal 008 Jumbotags® (Dalton Supplies Ltd, Henley-on-Thames, UK). Throughout each year, all MI beaches where elephant seals regularly haul out were searched for seals every 7–10 days, and the numbers of all untagged and tagged seals were recorded. For every tagged seal that was resighted (including non-MI tags), the date and locality of the sighting, tag colour combination and three-digit number were recorded to identify the seal (see de Bruyn et al. 2008, Oosthuizen et al. in press for details).

PEI summer surveys

Elephant seal surveys at PEI were conducted during 17–22 December 2001, 18–19 November 2004 and 16–20 December 2008. The November survey, which coincided with the end of the breeding season and the onset of the juvenile moult, presented the only opportunity for the marking of weaned pups at this locality to date (Bester and Hofmeyr 2005). The timing of the two December surveys corresponded with the peak moult haulout period for subadult males and subadult to young adult females (Kirkman et al. 2003). The survey area covered most of the coastline where elephant seals are likely to haul out, from Kent Crater in the north-west to Ross Rocks Peninsula in the north-east, and from Wandering Albatross Valley in the east to McNish Bay in the south-west (Figure 1), with the following exceptions: in the 2001 survey, it was not possible to check all the likely moulting sites in the Penguin Beach surroundings for seals, due to a lack of time and manpower; in 2004, only Wandering Albatross Valley to McNish Bay was surveyed. During the 2004 survey, 90 of the 130 weaned pups encountered were double-tagged (Bester and Hofmeyr 2005).

We noted the number of seals present at each site, seals that could be inspected for the presence of tags, and those with tags. For all seals with tags, attempts were made to record tag–resight data (as described above for MI). Untagged seals were subjectively classified by experienced observers as weaned pups, under-yearlings, yearlings, subadults, adult females and adult males, using morphological comparisons with known-aged seals from MI. In some cases, beach topography, or breeding colonies of Subantarctic fur seal *Arctocephalus tropicalis* and Antarctic fur seal *A. gazella*, prevented access to elephant seals. In such cases, we only noted the number of seals present without conducting tag resights.

Analyses

The MI-resighting history of each tagged individual that was observed at PEI during any of the summer surveys was scrutinised. For each of these individuals, it was first determined whether or not it had been recorded as present at MI during each moult season between birth and the last time it was resighted alive, including the year(s) that it was observed on PEI. 'Seal years' between the last resighting record of an individual and the end of the study (April 2009) were disregarded because the status of the animal (e.g. alive, dead or permanently emigrated) would have been uncertain during this period. A seal year corresponds to 15 October$_{(t)}$ to 14 October$_{(t+1)}$, because it was assumed that the seals aged a year on 15 October, the peak haulout date for breeding females at MI (Kirkman et al. 2004). Annual capture probabilities (as used in the estimation of annual survival estimates, e.g. Pistorius et al. 1999) were calculated for each of these individuals, taking all haulout phases during a year into account and treating multiple sightings within a year as a single sighting.

To determine whether or not the MI resight histories of the MI-tagged seals recorded at PEI are typical for individuals of the MI population, we compared this dataset to a simulated dataset (10 000 replications) based on individuals selected at random from corresponding birth cohorts. Individuals observed at PEI during summer surveys, as well as individuals that were never resighted after their first year, were excluded from the simulation. The observed and simulated groups were compared by calculating the capture probability: $P = X/n$, where X represents the number of 'successes' (present at MI) in n possible years. Proportions were taken over the total sample size and not individual seals (i.e. the sampling units; see Crawley 2007). Analyses were performed in R 2.9.1 (R Development Core Team 2009) and probabilities were considered statistically significant at $p < 0.01$.

Results

Resights of MI seals at PEI

The timing of the PEI surveys corresponded to early stages of the moult season, with yearlings and subadults being the age classes that were best represented in the counts (Table 1). In total, 42, or 10% of the 416 seals inspected for tags at PEI, were tagged as weaned pups at MI (Table 2). Additionally, three seals tagged at PEI in 2004 were encountered at PEI. Thirty-eight of the resighted MI-tagged seals could be individually identified; the other four individuals were not identified because their tag numbers could not be resighted with confidence. The proportion of seals inspected for tags that did have tags was similar between the two December surveys, when subadults were the predominant moulting group, but higher during the November survey, when yearlings were the predominant moulting group (Table 2). All tagged seals except one were associated with the moult haulout, the exception being an under-yearling (a recently weaned pup, FB269) recorded on 18 December 2008 that had been recorded at MI shortly before on 11 December 2008. The sex ratio among the resighted tagged seals (22 females, 17 males, 3 unidentified) was not significantly different to parity ($\chi^2 = 0.65$, df = 1, $p = 0.42$).

Life-history comparisons

Resight histories of the 37 MI-tagged seals that were recorded moulting at PEI totalled 119 seal years (115 moult seasons; birth to last known age alive) up to 2009. Moulting occurred at PEI in 37 (32%) of these years, and at MI in 46 (40%). A further 32 (28%) of the moult seasons were unaccounted for (absent from MI, possibly present at PEI, but no resights made; Figure 2). The simulations based on individuals selected randomly from the same birth cohorts showed that MI-tagged individuals were recorded as present at MI at the time of the moult during 77 ± 6% of seal years (mean ± SD, 10 000 replicates; Figure 2). The total moult attendance (40%) of the MI-tagged seals that were recorded moulting at PEI falls well outside the normal distribution range of the simulated sample ($Z = 37.51$, 2.5th percentile = 64.86%, 97.5th percentile = 87.49%, $p < 0.01$). When resights made during all haulout phases within a year were considered, the probability of observing the MI-tagged seals recorded at PEI increased to 58% per annum. However, this is still significantly lower than the annual recapture probability for the simulation (80 ± 4%, $Z = 33.46$, 2.5th percentile = 72.69%, 97.5th percentile = 87.66%, $p < 0.01$).

Table 1: Age class distribution of southern elephant seals (marked and unmarked) encountered at Prince Edward Island during three summer surveys

Survey period	Adult males	Adult females	Sub-adults	Yearlings	Under-yearlings	Weaned pups	Unknown	Total
December 2001	5	29	61	22			41	158*
November 2004	10	15	32	42		130		229
December 2008		23	150	32	4		37	246

* Undercount

Table 2: Number of tagged southern elephant seals encountered during three summer surveys at Prince Edward Island. MI and PEI tags indicate seals tagged at Marion Island and Prince Edward Island respectively

Survey period	Seals observed	Seals inspected for tags	MI tags	MI tags identified	Proportion: MI tag/untagged	PEI tags
December 2001	158*	117	9	8	0.077	
November 2004	229	90	18	16	0.200	
December 2008	246	209	15	14	0.072	3
Total	633	416	42	38		3

* Undercount

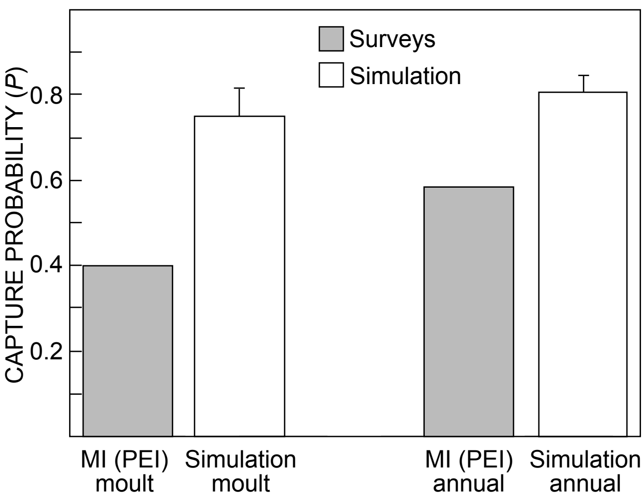

Figure 2: The moult and annual capture probabilities of MI seals resighted at Prince Edward Island (PEI) during three summer surveys compared with the capture probabilities of a random MI population simulation (10 000 replicates; error bars denote +SD). Seals recorded moulting at PEI have significantly lower MI-capture probabilities, even when all haulout phases within a year are considered

Resights of PEI seals at MI

Over a period of five years, 32 of the 90 weaned pups tagged at PEI hauled out on MI as immature seals to rest during autumn–winter (n = 40 occasions) and moult (n = 28 occasions). Males (n = 20) outnumbered females (n = 10), but this is unsurprising because nearly twice as many males (n = 57) as females (n = 29) were initially tagged at PEI. In all, 15 PEI-tagged seals were observed during more than one haulout phase at MI (mean number of haulout phases of PEI-tagged seals at MI = 2.09 ± 1.67 SD, n = 32). One subadult male hauled out on MI during autumn–winter and the moult of every year (up to and including the moult of 2008) since its birth in 2004. None of the 29 PEI-tagged females bred at MI during 2007 or 2008 (at age 3–4 years). However, based on current survival estimates from MI (de Bruyn 2009), juvenile and subadult mortality would have reduced the surviving PEI-tagged female cohort to only approximately 10 individuals by this age. Only a single PEI female that previously hauled out at MI to rest in autumn–winter and to moult was known to be alive subsequent to the 2007 breeding season.

Discussion

Intra-archipelago movement

Southern elephant seals are good mark–recapture study subjects (Bester 1988). During the predictable haulout phases of the life cycle, it is relatively easy to mark large numbers of seals, whereas resighting of marked seals is facilitated by the high site fidelity that is characteristic of the species (Hofmeyr 2000). However, although island populations appear to be relatively isolated, movement between islands within an archipelago (e.g. between MI and PEI) or even movements between locations on larger islands, may hamper mark–recapture resighting schedules. Few study protocols are capable of incorporating such spatial variation (but see Baker and Thompson 2007 for a Hawaiian monk seal *Monachus schauinslandi* example) and, consequently, discrimination between mortality and emigration to alternative sites is often impossible. Mark–recapture estimates of southern elephant seal populations, including those at MI, are assumed to have little emigration bias due to high site fidelity by individuals (Pistorius et al. 1999). However, caution should be exercised when inferring site fidelity using data from individuals actually present at MI (de Bruyn 2009). Whereas Hofmeyr (2000) showed that site fidelity at an island scale (between different beaches on the same island) was high for seals returning to MI (i.e. seals usually haul out in the vicinity of their natal beach or site of first reproduction when they return to the island), these results excluded individuals that did not return to MI (de Bruyn 2009). High beach-specific, island-scale site fidelity of individuals returning to MI should therefore be distinguished from archipelago site fidelity, with associated temporary or permanent emigration between islands within the group.

The increased tag-ratio observed at PEI during the peak yearling moult is consistent with findings of reduced site fidelity of under-yearlings and yearlings at MI (Hofmeyr 2000) and peak dispersion of juveniles during the moult from Macquarie Island (van den Hoff 2001). No discernible sex difference among the MI juveniles that dispersed to PEI was observed or expected (Hofmeyr 2000), as opposed to breeding dispersal or long-range dispersal (e.g. between archipelagos), which are predicted to be male-biased (Slade et al. 1998). The occurrence of the recently weaned MI pup (FB269) at PEI is not unexpected; weaned pups are known to disperse between their natal sites and other haulout sites in the vicinity during the post-natal period ashore, before finally departing on their first true pelagic trip during late November and early December (Wilkinson and Bester 1990). At this time, untagged weaned pups are occasionally found at MI beaches as well. These seals most likely originate from PEI as all of the pups born at MI are tagged shortly after weaning, and under-yearlings from the Crozet Islands only haul out at MI from January onwards (Mammal Research Institute, unpublished data).

Intra-archipelago movement and the MI mark–recapture programme

The annual moult is obligatory for all elephant seals, but elephant seals of the MI population do not always moult at MI. This is illustrated by the animals observed moulting on PEI in this study, and the resighting histories of several other individuals that could be identified in the MI mark–resight database. For example, one tagged female (GW506) returned to MI to breed 12 times between 1992 and 2008, but was recorded only twice at MI during the moult over her 20-year lifespan. It is unlikely that she or other individuals that were not recorded during the moult were in fact present and escaped observation, considering the long duration of each individual's moult (approximately a month) and the intensive resighting effort at MI. Such individuals therefore most likely moulted at PEI or further afield (e.g. the Crozet Islands, Bester 1989). Given that site fidelity of returning MI-tagged seals is generally high (Hofmeyr 2000), as supported by the result of the random simulations in this study, individuals that disperse elsewhere for certain haulout phases appear to be the exception rather than the rule. However, it does emphasise the need to consider all the haulout phases for mark–resight based population studies of elephant seals. Also, where there are one or more neighbouring islands that animals may alternate between, studies should ideally include marking and resighting of individuals on all islands, because mark–recapture conducted at only one of the islands will most likely result in variable capture probabilities of individuals, even if all haulout phases are considered.

The fact that some elephant seals disperse from MI to PEI during the moult does not necessarily result in permanent emigration from the MI population. Most of these seals are also observed at MI, although at a lower incidence than a random population sample. Temporary emigration from the study area violates the mark–recapture Cormack-Jolly-Seber (CJS) model assumption, that every marked animal present in the population at time i should have the same probability of recapture P_i (Pledger et al. 2003). However, absence from MI during the moult is mitigated by the fact that resights of individuals obtained during all haulout phases (moult, resting or breeding) are condensed to a single-encounter history event per seal year. Heterogeneity in capture probability will only result if some individuals that are known to still be part of the MI population are not resighted at all during one or more years. This is most likely to occur for immature seals (which do not yet breed), because absence of this age class from MI during the moult has been shown to be also associated with absence during the autumn–winter resting phase (Pistorius et al. 2002). Variation in the moult haulout attendance also has implications for seasonal (intra-annual) comparisons of survival, for which absence during a haulout phase would not be diluted by presence in another phase, as in inter-annual comparisons (e.g. Pistorius et al. 2008).

Conclusion

The tag resights made during the three summer surveys at PEI, and the tagging of samples of seal pups at PEI, permitted investigation of moult dispersion patterns of mostly immature seals between MI and PEI. Our ability to assess the rate at which MI seals emigrate temporarily or permanently to PEI was constrained by the low, infrequent resight effort at PEI, which was limited to a single haulout phase and biased towards immature age classes. A more systematic approach to surveying PEI elephant seals will be necessary to understand the extent of migration between the two islands, and address concerns associated with unequal mark–recapture effort between islands of an archipelago (e.g. Baker and Thompson 2007). The sampling design should include survey coverage of other haulout phases, especially the breeding season, and permit marking of weaned pups at PEI and assessment of breeding dispersal between the islands.

Acknowledgements — We thank Mark Hindell for assistance with the simulation model, and John van den Hoff and Steve Kirkman for their insightful comments on an earlier draft of the manuscript. We thank the Department of Environmental Affairs for logistic support and the Branch Marine and Coastal Management for setting up the summer surveys, under the leadership of Robert Crawford. Peter Ryan, Bruce Dyer and Johan Visagie variously assisted with overall counts during the summer surveys. Permission to visit Prince Edward Island was granted by the Prince Edward Islands Management Committee. While compiling this manuscript, WCO received financial support from a National Research Foundation grant-holder-linked bursary within the project: Conservation of Seabirds, Shorebirds and Seals, led by Les Underhill of the Animal Demography Unit, Department of Zoology, University of Cape Town.

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