

Aggregation and dispersion of female New Zealand sea lions at the Sandy Bay breeding colony, Auckland Islands: How unusual is their spatial behaviour?

A.A. Augé^{1,2,6)}, B.L. Chilvers³⁾, A. Moore⁴⁾, R. Mathieu^{1,5)}
& B.C. Robertson²⁾

(¹ Spatial Ecology Research Facility, School of Surveying, University of Otago, P.O. Box 56, Dunedin, New Zealand; ² Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand; ³ Marine Conservation Unit, Department of Conservation, P.O. Box 10-420, Wellington, New Zealand; ⁴ Information Science Department/School of Surveying, University of Otago, P.O. Box 56, Dunedin, New Zealand; ⁵ Earth Observation Research Group, Natural Resources and Environment, CSIR, P.O. Box 395, Pretoria 0001, South Africa)

(Accepted: 16 February 2009)

Summary

We investigated the spatial behaviour adopted by female New Zealand sea lions, *Phocarctos hookeri*, at the Sandy Bay breeding colony in 2002 and 2003. Each breeding female exhibited a spatio-temporal behaviour based on two phases: breeding and dispersion. The breeding phase, typical of all otariids, led to the formation of the breeding aggregation where all pupping took place. Each female later moved outside the breeding area and entered a dispersion phase. The female population spread inland, and progressively decreased as females took their pups away from Sandy Bay. Pup survival was not affected by this spatial behaviour though the year had an effect. A larger population size during one year may have created a dilution of male aggressiveness and resulted in fewer movements of females. Females that had to move more during the pupping day were found to be more likely to lose their pups. Although a few studies have shown that mother and pup pairs of other species may exhibit dispersal after breeding, the observed terrestrial dispersion phase of the female New Zealand sea lions has never been reported for any other pinniped species and is likely unusual.

Keywords: aggregation, dispersion, movements, New Zealand sea lion, spatial behaviour.

⁶⁾ Corresponding author's e-mail address: augam928@student.otago.ac.nz

Introduction

Aggregations are common amongst animal species and can be divided into two types: temporary and permanent. While permanent aggregations are more often related to safety from predators, family groups, extreme sociality or resource locations, seasonal aggregations more often specifically aim at breeding or migrating (Tinbergen, 1965; Parrish & Edelstein-Keshet, 1999; Siiter, 1999). Seasonal breeding aggregations are typical of most pinnipeds, including all otariids (fur seals and sea lions), but excluding some ice-breeding seals (Boness, 1991). This temporary breeding aggregation behaviour is shared with seabirds. These two groups have in common a singular life history made of an absolute segregation between foraging and breeding areas. This is thought to have led to the evolution of their temporary breeding colonies, where individuals gather to mate and breed (Parrish & Edelstein-Keshet, 1999). However, while seabirds are monogamous, pinnipeds are highly polygamous and males exhibit no parental care of offspring (Boness, 1991).

Group-living individuals generally face a trade-off, as both benefits are gained and costs arise in animal aggregations (Parrish & Edelstein-Keshet, 1999). Forming large groups increases the competition for resources, enhances the spread of diseases and parasites, and can create aggregations of predators. A critical group size exists at which the benefit of living in aggregations exceeds its cost for an average individual (Parrish & Edelstein-Keshet, 1999).

In polygamous pinnipeds, because males compete to gain access to and restrain the females, harassment, injury and death are extra costs for females to stay in a breeding aggregation (Cassini & Fernández-Juridic, 2003; Chilvers et al., 2005). Pups may be harassed and killed by males, increasing the potential cost for the reproductive success of females (Campagna et al., 1992; Wilkinson et al., 2000). Harassment that forces non-essential movements by breeding females also may impact their nursing capabilities, i.e., energy loss from milk production, shorter periods onshore, ineffective recognition process between mother and pup, intermittence of suckling bouts and isolation of the pup from its mother (Peterson & Bartholomew, 1967; Trillmich, 1990; Bowen, 1991; Campagna et al., 1992; Boness et al., 1995; McCulloch & Boness, 2000), and ultimately affects pup survival. The process of recognition between mother and pup, the imprinting, is especially vital for

the survival of the pup, and seems to happen during the first day after birth in pinnipeds (Lawson & Renouf, 1987; Gisinier & Schusterman, 1991). Consequently, we hypothesise that movements of females on this day affect the survival of the pups.

Cassini (2000) developed a model of cost-benefit for the formation of breeding colonies in pinnipeds, which was later tested (Cassini & Fernández-Juridic, 2003). The model predicts that females form high-density breeding aggregations, primarily to limit male harassment and aggression. In larger groups of females, male harassment should be diluted and, thereby, increase the reproductive success of individual females.

The New Zealand sea lion, *Phocarctos hookeri*, forms temporary breeding aggregations in December and January each year (Marlow, 1975; Robertson et al., 2006). Females give birth, exhibit a perinatal period and start alternating foraging trips at sea with time onshore in these aggregations (Marlow, 1975). After dominance interactions, successful adult males establish themselves within a group of females, defending small areas around them between which females can move freely (Marlow, 1975). Other adult males and sub-adult males stay at the periphery of the breeding area waiting for one of the males to leave or be defeated (Marlow, 1975). All males, both within the group of females or at the periphery, may be aggressive. Marlow (1975) described the forced movements of females as the major disturbance of male harassment, but injuries and deaths can happen (Chilvers et al., 2005).

The breeding aggregation ends when all females have pupped and mated, which occurs within a week after birth (Marlow, 1975). The adult males leave Sandy Bay while sub-adult males remain (Marlow, 1975). Female New Zealand sea lions nurse their pups for at least 8 months, alternating foraging trips at sea with nursing periods onshore. For otariids inhabiting medium latitudes, this is a common length of time for nursing (Bowen, 1991). However, there were anecdotal reports of an unusual spatial behaviour after the breeding period and they constituted the starting point of this study.

Individuals of most pinniped species are rarely found more than 100 m from shore (Evans & Raga, 2001), yet Eden (1955, p. 35) wrote that "It is interesting to note that sea-bears [female New Zealand sea lions] in particular penetrate considerable distance inland [...]". Several other expeditions found females and pups inland with sightings up to 2 km from the nearest access to the ocean during the non-breeding period (Marlow, 1975; Mackworth & Munce, 1999; McNally et al., 2001). Consequently, it appears that

once the breeding ends female New Zealand sea lions can disperse inland to an unusual extent. These movements are initiated by the females not by the pups (personal observation). Nonetheless, to date, no research has investigated the terrestrial spatial behaviour of the female New Zealand sea lions in detail.

The aims of this research were to (1) describe and quantify the spatial behaviour adopted by the female New Zealand sea lions at a breeding colony; (2) test for potential effects of the spatial behaviour and movements of females on pup survival; and (3) detect a potential impact of the population size on the spatial behaviour of females.

Materials and methods

Study colony and sample population

We conducted the research at Sandy Bay (50.5°S 166.3°E), on Enderby Island, in the Auckland Islands, New Zealand (Figure 1). The study area covered 0.7 km² and included a 400 m long sandy beach, backed by a large sand dune. The sandy beach, approx. 40 m wide, is the site where New Zealand sea lions breed each year. In this study, the term breeding area refers to the area where all births and mating occurred. Access from the ocean to

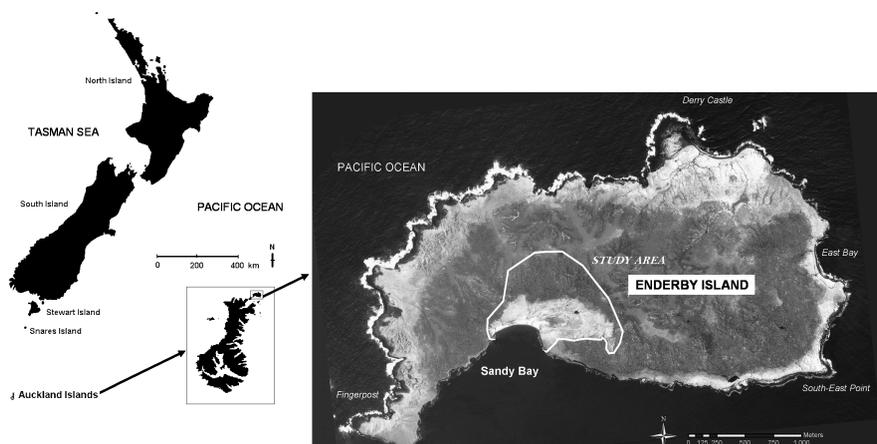


Figure 1. Study area at Sandy Bay, Enderby Island, in the Auckland Islands (New Zealand sub-Antarctic islands).

the study area by sea lions was restricted to the sandy beach as cliffs surround this area.

An average of 420 pups ($N = 27$, $SD = 47$) has been produced per year since the first official count in 1966 at Sandy Bay (Childerhouse & Gales, 1998; Chilvers et al., 2007). In 2000, the New Zealand Department of Conservation branded 135 adult breeding females (Wilkinson et al., in press). These females comprised our sample population as they were easily identifiable in all weather conditions. The fieldwork was conducted during two years. In 2002, 88 branded females used Sandy Bay, or 21.8% of the total female population, and 89 in 2003 (18.2%; Chilvers et al., 2007). During each year, from 8 December until 20 January, we recorded the daily numbers of females at Sandy Bay by manual counts conducted from a vantagepoint overlooking the colony. During our study, these females were 6 to 18 year-old, all of breeding ages. All pups of branded females were marked the day after birth using small flexible plastic caps glued to the fur of their heads with non-toxic fast-setting cyanoacrylic glue (Loctite 454). Pup deaths were recorded with a precision of one day. Females were separated into three categories depending on their breeding status: those with a pup that survived until the end of the study (BReeding Alive pup or BRA), those with a pup that died during the study (BReeding Dead pup or BRD), and those that did not breed during the year (Non Breeding or NB). In 2002, there were 59 BRA, 14 BRD and 15 NB, while in 2003, there were 66 BRA, 12 BRD and 11 NB.

Acquisition of female locations

We recorded the locations of the branded female New Zealand sea lions once every day in the study area, for 75 days in 2002 (due to logistic reasons the expedition could not last longer), and for 106 days in 2003, starting on 6 December of the preceding year. The sampling rate of locations of individuals (every 18 to 27 h) assured the independence of the measured locations, both amongst females and within the dataset of each female. Female New Zealand sea lions commonly went back to sea to feed between two records of locations, except during the perinatal period. When females stayed on-shore between two consecutive locations, they were able to walk hundreds of meters to choose or change resting or nursing sites (personal observation). Their locations were considered as independent. Using sketch maps

and a handheld Garmin 12 GPS (Garmin International, USA), an observer conducted daily surveys of the study area and recorded the locations of all branded females and the presence of a pup. We assumed that the location where the first record of a female was made with a pup corresponded to the site of pupping. When females were in the breeding area, the observer drew sketch maps from a vantage point overlooking the colony. We later derived the females' locations using fixed GPS points of visible objects (e.g., rocks, sticks) along the beach. The overall accuracy of the points depended on the accuracy of the handheld GPS, on average 7 m, with the precision of the locations within the breeding aggregation of around one female length (1.5 m). A total of 1828 and 2424 daily locations of branded females were taken during 2002 and 2003, respectively.

Data analyses

In order to analyse the spatio-temporal pattern of the data, all GPS locations of females were integrated into a Geographic Information System (GIS; Arc-GIS, ESRI, Redlands, CA, USA) database with tag number, status and date in numeric format as attributes. All non-spatial statistical analyses were conducted in SPSS 14.0 for Windows (SPSS, Chicago, IL, USA).

The presence of female New Zealand sea lions at Sandy Bay is a temporary phenomenon. Their number also varied during the study. We used $F(x)$, the total number of females in the breeding area on day x (manually counted until 20 January each year), and $B(x)$, the number of branded females in the breeding area on day x (available for each day of the study) to produce the daily ratios of branded females (F/B). The mean of these ratios, r , was determined for each year, and used to estimate F after 20 January ($F = B \times r$). Outside the months of fieldwork, we investigated the presence of females at Sandy Bay through results, notes or reports from previous expeditions.

We described the temporal use of Sandy Bay by adult female sea lions for each year by calculating the median first day of presence, the mean length of the perinatal period, the median date of pupping, the median last day of presence, and the mean total number of days of presence. In order to quantify the spatial behaviour adopted by female New Zealand sea lions, we conducted point pattern analyses on the locations. Each female's location dataset was first tested for spatial autocorrelation using the Moran's I coefficient (Goodchild, 1986). Grids of 10 m resolution were placed over individual's locations, the grid extent being the minimum bounding box. Each cell was coded

either 'present' or 'absent'. Moran's I formula ascertained if the pattern of presence-absence of the females was spatially autocorrelated.

The Nearest Neighbour Index (NNI) is commonly used to characterise the distribution pattern of wildlife, giving the spatial relationship within a set of points, from aggregation (total aggregation; $\text{NNI} = 0.00$) to dispersion (uniformity; $\text{NNI} = 2.15$) of the points compared to a random Poisson distribution ($\text{NNI} = 1.00$) (see Clark & Evans, 1954; e.g., Khaemba, 2001; Kirby & Abraham, 2003). In the present study, we used NNIs, first, as indicators of the spatial distribution of locations of the female population and second, as indicators of the spatial behaviour of specific individuals over time. NNIs were determined with the study area, S , the total number of locations, N , and the distance to the nearest location for each location, d , as in equation (1):

$$\text{NNI} = \frac{\sum_{i=1}^N d}{N} / 0.5\sqrt{\frac{N}{S}}. \quad (1)$$

For each NNI, a Z -score and its related P -value were calculated to test the significance of the pattern observed as described in Clark & Evans (1954; where Z is named c). For some individuals, the number of locations was small. We only used females with at least six locations for each NNI calculated. All locations taken after the 18 February (end of first year) were disregarded to obtain NNIs during the same period each year and allow comparisons between the two years.

Firstly, the spatial behaviour of the females was investigated at the population level over time. For different periods, we plotted the locations of all females and calculated the associated NNI values. The highest densities of females within the breeding aggregation were determined for later comparison with other species. The density was obtained with the Minimum Convex Polygon (MCP; see Mohr, 1947) area (in m^2) of all of the females' locations during the survey divided by the associated total number of females on the same date. Secondly, at the individual level, the NNIs were calculated for the breeding phase and for the dispersion phase of each breeding female. All terms related to breeding females' behaviour and used in this study are illustrated in Figure 2. From the locations of males considered as 'territorial' (i.e., those who mated with females; B.C. Robertson, unpublished data), we delimited the breeding area for each year with the MCP of all these locations. Breeding females were considered in their breeding phase until they were recorded outside the breeding area, at which point they entered their dispersion

to compute the distances between two consecutive locations (Beyer, 2004). This function creates a matrix of all inter-point Euclidean distances from a dataset of points. From this matrix, the distances between consecutive days of the perinatal period were manually extracted for each female as the date of pupping and length of perinatal period individually varied.

To test the main hypothesis that the movements of a female on the pupping day (during which imprinting likely occurs) influenced the survival of her pup, we produced a Univariate GLM with two fixed factors: Year (two levels: 2002 and 2003) and Status (two levels: BRA and BRD). In order to exclude the possibility that the movements on prior or later days also affected the survival of the pups, the same analysis was conducted for the days before pupping and the days after pupping. All required conditions were met: normality of distribution of residuals (Kolmogorov–Smirnov test with Lilliefors significance) and equality of variances (Levene's test). We related the factor Year to population size because it was the main difference between the two study years. Any difference between years was consequently interpreted as an effect of population size.

Results

Temporary presence of female New Zealand sea lions at Sandy Bay

The presence of female New Zealand sea lions at Sandy Bay is an annual cyclic phenomenon that starts with the formation of the breeding aggregation and ends after all females have left with their pups (Figure 3). The presence of females was initiated on 30 November and 1 December, during 2002 and 2003, respectively, when the founder females (a lone female and a group of three, all expectant) landed on the beach at Sandy Bay. A rapid increase in the number of females onshore followed with a similar pattern each year. The maximum density of females in the breeding area were recorded on 23 December (87 females/100 m²) during the first year and on 20 December during the second year (85 females/100 m²). The number of females using Sandy Bay then progressively diminished until the end of March. The mean ratio of branded females, r , was estimated at 7.61 (95% C.I. 7.04–8.19) during 2002 and at 7.72 (95% C.I. 7.37–8.06) during 2003.

We did not investigate the use of Sandy Bay by New Zealand sea lions outside the period of December to March. However, we recorded no female

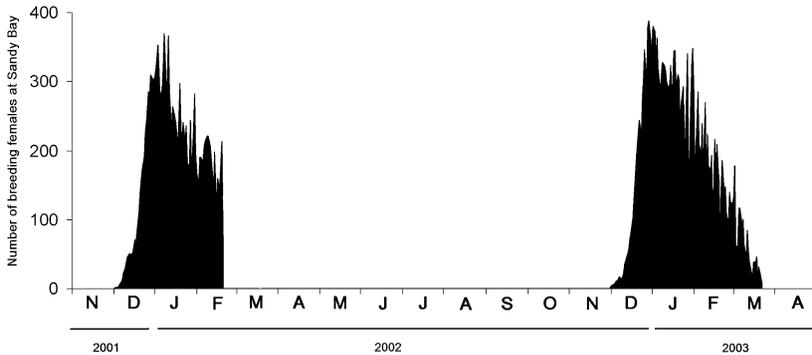


Figure 3. Cyclic presence of the female New Zealand sea lion population at Sandy Bay, Enderby Island, Auckland Islands, between November 2001 and April 2003. The fieldwork was conducted from 4 December 2001 until 18 February 2002 and from 4 December 2002 until 25 March, 2003. The fieldwork was stopped earlier in 2002 but the population likely decreased similarly to the second season (not represented on the graph). The absence of females outside the fieldwork was based on the expeditions' observations at arrival and departure and reports of other expeditions throughout the year.

onshore upon arrival at Sandy Bay and only an estimated eight females (one branded female) in the study area at the end of the expedition in 2003. Records of preceding expeditions at Sandy Bay during various periods of the year all confirm the absence of female New Zealand sea lions from Sandy Bay outside the summer months (Eden, 1955; Marlow, 1975; I. Wilkinson, personal communication, 2006).

The average breeding female first arrived at Sandy Bay on 21 December, pupped on 26 December, and exhibited a perinatal period of 8 days including approx. 6 days after the pup was born (Table 1). Any differences amongst females and between years in the timing of behaviours were minimal. However, the date of final departure with pups to another nursing site varied amongst females (Table 1). One female moved her pup away from Sandy Bay soon after birth (23 days), whereas other females left their pups at Sandy Bay for up to 68 days. For comparison, we also illustrated the results for the females that did not breed during one year (Table 1). The non-breeding females were present during most of the period during which we observed the female New Zealand sea lion population, although they were not part of the founder females' group. On average, non-breeding females used Sandy Bay only half as frequently as breeding females (15.27 versus 31.64 days).

Table 1. Means and median dates of the main events for female New Zealand sea lions, *Phocarctos hookeri*, at the Sandy Bay breeding colony.

	First day at SB	Perinatal period (in days)	Part with pup (in days) ^a	Date of pupping	Last day at SB ^b	Total number of days at SB ^b
Breeding females, <i>N</i> = 177						
Mean number		8.25	6.28			31.64
SD (in days)		3.03	3.06			8.19
Median date	21 Dec			26 Dec	1 Mar	
AbsD (in days)	6.04			5.53	7.60	
Min 2002	2/12/01	1.00	0.00	7/12/01	–	–
Min 2003	6/12/02	2.00	0.00	8/12/02	26/12/02	14.00
Max 2002	6/01/02	14.00	13.00	8/01/02	–	–
Max 2003	6/01/03	15.00	14.00	8/01/03	21/03/03	61.00
Non-breeding females, <i>N</i> = 26						
Mean number		–	–	–		15.27
SD (in days)						5.75
Median date	26 Dec				21 Feb	
AbsD (in days)	8.95	–	–	–	11.29	
Min 2002	8/12/01	–	–	–	–	–
Min 2003	16/12/02	–	–	–	2/02/03	8.00
Max 2002	9/02/02	–	–	–	–	–
Max 2003	3/02/03	–	–	–	17/03/03	26.00

AbsD: Absolute Deviations of medians.

^a Number of days of the perinatal period after the pup was born (including pupping day).

^b Only results from 2003 were used as the fieldwork ended earlier in 2002.

Nearest Neighbour Index (NNI) as a measure of spatial behaviour

The locations of a female were not spatially autocorrelated (mean Moran's *I* value = 0.03 with 95% C.I. 0.00–0.07 and range –0.08 to +0.27) and the use of subsequent spatial analysis methods was consequently deemed appropriate. At the population level, a spatio-temporal pattern clearly appeared with the occurrence of the breeding aggregation until around 18 February when the females' locations started spreading inland (Figure 4). The behaviour of the female population was consistent between years. The breeding aggregation appeared during both years in December, followed by a similar progressive spread of the females' locations. The NNIs for each period illustrated this pattern, with values close to 0 (aggregation) from 6 December

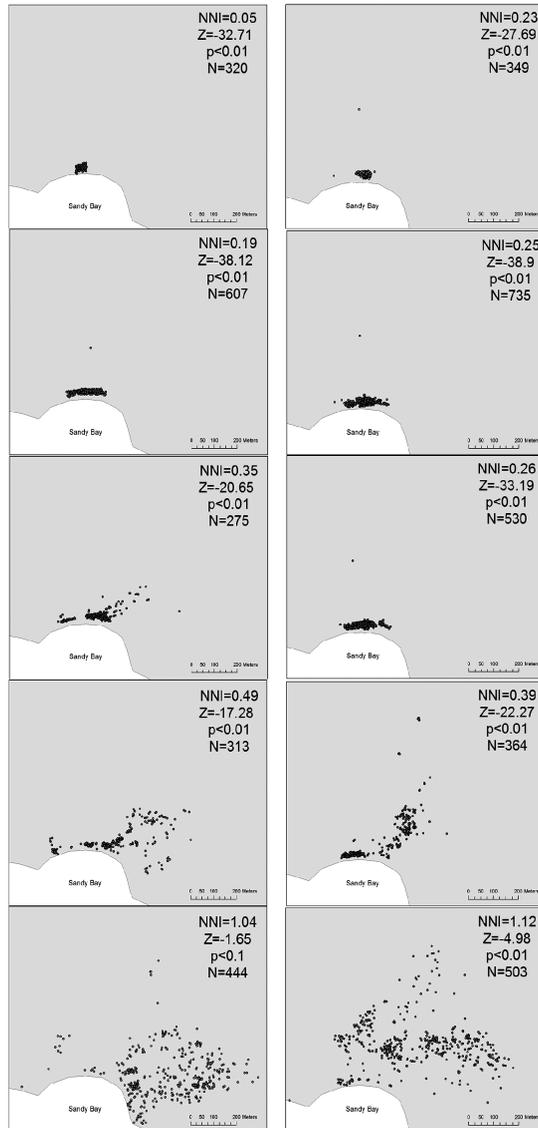


Figure 4. Locations over time, and associated NNI, statistical significance (Z and P) and number of locations (N) of the population of female New Zealand sea lions at Sandy Bay during year 2002 (left column), and year 2003 (right column). From top to bottom: period 1 December to 25 December, period 26 December to 9 January, period 10 January to 18 January, period 19 January to 29 January, period 30 January to 18 February. Note that females' locations were up to 620 m inland on the 18 February. In March 2003 (not shown here) females reached inland locations up to 800 m (straight line) to the nearest access to the water.

until 18 January and values of up to 1.65 (dispersed) from 30 January to 18 February (see Figure 4).

At the individual level, the median dispersion date for breeding females was 20 January (range 2 January–4 February) during 2002 and 22 January (range 28 December–7 February) during 2003. The number of locations for each female during the breeding phase ranged between 6 and 31, and 6 to 25 during the dispersion phase. Non-breeding females could be found in or outside the breeding area after a first group of breeding females dispersed. We considered all the locations of non-breeding females as a dispersion phase (range 6–21). Figure 5 presents examples of the typical distribution of a female's locations during one year and the associated NNIs for each of the three statuses.

The result of the GLM showed that all three factors (Phase, Year and Status) had an effect on the NNIs, with no interaction between factors (Table 2). The locations of breeding females during their breeding phase were aggregated (NNI close to 0), whereas they were randomly sparse during the dispersion phase (NNI close to 1; Figure 6). The distributions of the individual females' locations were also more dispersed during 2002 than during 2003 (Figure 6). For the factor Status, the NB level was found to be the only source of the effect (Bonferroni test: for NB \times BRA and NB \times BRD, $p < 0.001$; for BRA \times BRD $p = 0.292$). There was no effect of Status on the NNIs amongst breeding females (BRA and BRD) whereas NNIs of non-breeding females significantly differed from those of breeding females. Non-breeding females had higher NNIs (sparser locations) than breeding females (Figure 7). The distribution of the locations of a breeding female was consequently not found to affect the survival of her pup. However, breeding females exhibited a different spatial behaviour than non-breeding females, which had no breeding phase and sparser locations overall. For the non-breeding females, the mean NNI was 1.60 (SD = 0.77) in 2002, closer to uniformity.

Movements of breeding females during the perinatal period

All females, and during both years, reduced their movements on pupping day (Figure 8). While during day 1 and day 2 the distances were still lower than before pupping, the females progressively increased the distances they moved after pupping day.

As hypothesised, the distance moved by a female on the pupping day influenced the survival of her pup (Table 3). During the pupping day,

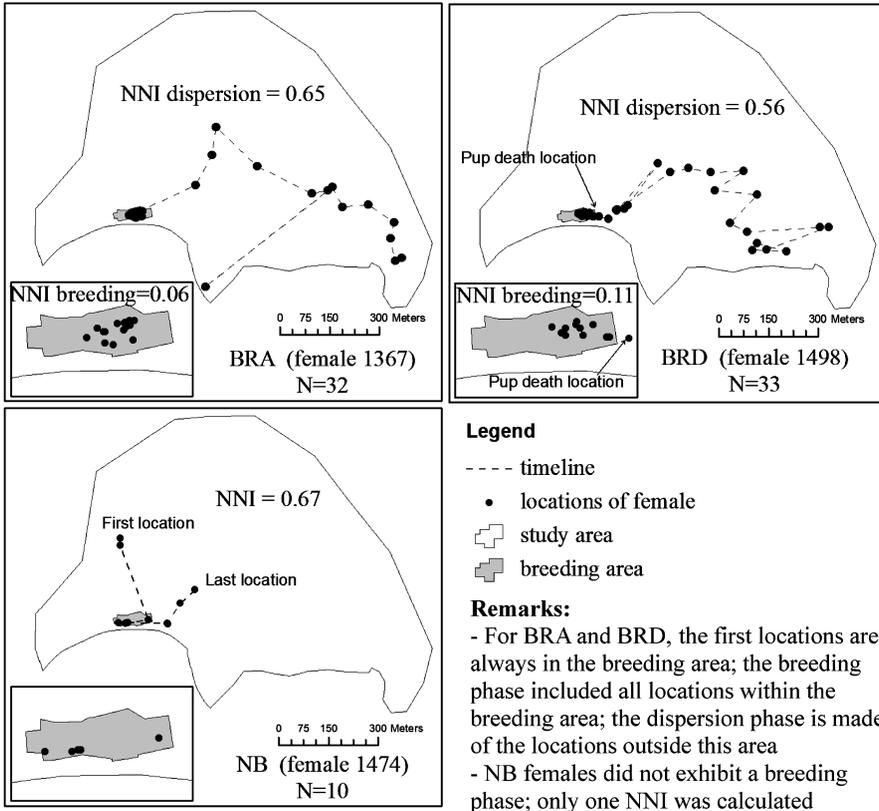


Figure 5. Illustration of the typical spatial behaviour of individual female New Zealand sea lions at the Sandy Bay breeding colony: locations, timeline and associated NNI for breeding and dispersion phases, for each status with the example of female 1367 as BRA (female that had a pup that survived), female 1498 as BRD (females whose pup died before the end of the study) and female 1474 as NB (female that did not pup) during 2003. The box shows a close-up of the breeding area. The dates of dispersion were 17 January and 20 January, respectively, for females 1367 and 1498. The breeding area was where all pups were born and mating took place. The timeline (dashed line) is an indication of the timing of the locations and does not represent movements of females (females usually went to a foraging trip between consecutive locations).

more females who later lost their pups (BRD) had moved greater distances (mean \pm SD = 8.9 ± 6.6 m) than females whose pups survived (BRA; mean \pm SD = 6.3 ± 4.2 m) with no effect of the year. There was no effect of the distances moved by females for the pup survival for the other days of the perinatal period (see Table 3). However, there was a significant difference in the distances that breeding females moved during the days after

Table 2. Univariate GLMs for the variable NNI, with three fixed factors: Phase (two levels: breeding and dispersion), Year (two levels: 2002 and 2003) and Status (three levels: BRA, BRD and NB).

Source of variation	df	<i>F</i>	<i>p</i>
Corrected model	9	131.553	<0.001
Phase	1	562.325	<0.001
Year	1	27.107	<0.001
Status	2	6.597	0.002
Phase × Year	1	0.115	0.735
Phase × Status	1	0.548	0.460
Year × Status	2	1.772	0.172
Phase × Year × Status	1	0.025	0.874

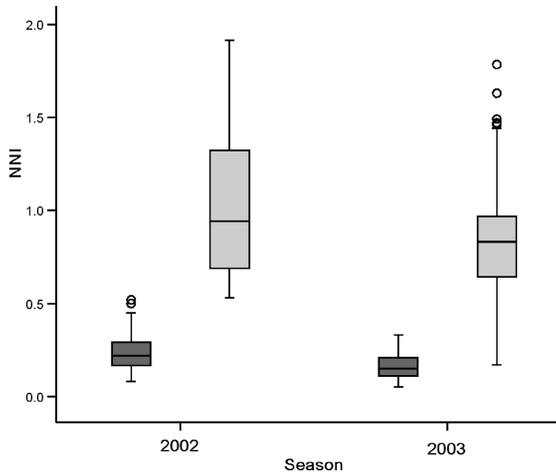


Figure 6. NNIs during the breeding phase (dark grey boxes) and the dispersion phase up to 18 February (light grey boxes) during years 2002 and 2003 for all breeding females at Sandy Bay. The box plots display the medians, quartiles, ranges and outliers.

pupping between the two years. Females overall moved more in 2002 than in 2003 (see Figure 8).

Discussion

Spatial behaviour of female New Zealand sea lions at Sandy Bay

In 2002 and 2003, the New Zealand sea lion female population was present at Sandy Bay from December to March. During this period, a two-phase

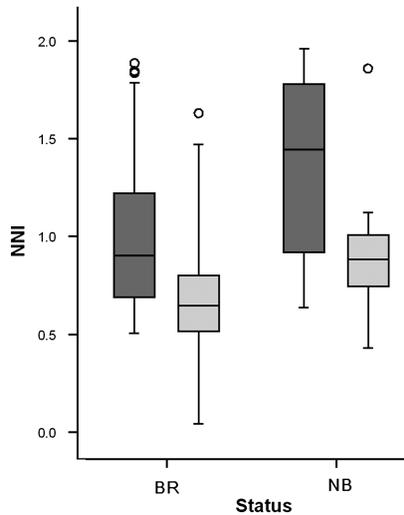


Figure 7. Differences in NNIs between years 2002 (dark grey boxes) and 2003 (light grey boxes) for breeding females (BR) and non-breeding females (NB) calculated with locations taken before 18 February. The box plots display the medians, quartiles, ranges and outliers.

pattern (breeding and dispersion) was the characteristic spatial behaviour adopted by the breeding females. All females gave birth to their pups within the breeding aggregation. Then each female started, at various dates (range 28 December–7 February), a dispersion phase that led to the progressive disappearance of the breeding aggregation as the female population spread inland. Towards the end of the study, in March 2003, the female population was spread within the study area with a NNI of 1.12 (significantly dispersed locations). Each female also dispersed her locations over time within a large area with NNI up to 1.93 (close to uniformity). However, females still formed small sparse groups and did not seem to repel each other. This would have been indicated by a NNI closer to 2.00 at the population level (uniformity of spatial distribution of the locations).

The events taking place during this pattern (including arrival in the breeding area, pupping, perinatal period, and highest density) were consistent between the two study years. The time of pupping was previously known to be very constant based on a time-series dataset of 25 years (Wilkinson et al., 2003; Chilvers et al., 2006). The breeding aggregation started forming in early December, when the founder females came ashore on the sandy beach at Sandy Bay. In this group, females were densely aggregated with a peak

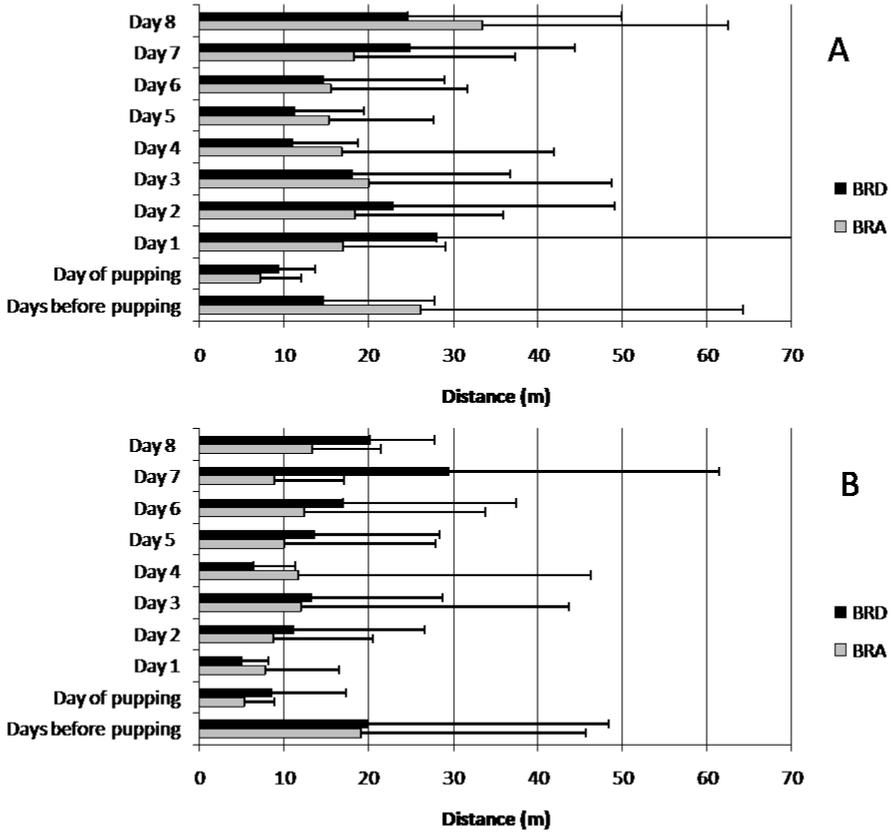


Figure 8. Distances moved by breeding females (BRD and BRA) during the perinatal period, showing the mean daily distances moved during the days before the pupping day (mean of all days), during the pupping day and from day 1 up to day 8 in 2002 (A) and 2003 (B). The bars show the positive SD (in graph A, Day 1 of BRD, the value is 92 m).

density of 87 females/100 m², which is common for otariids (Boness, 1991). A permanent accretion of females coming back from foraging trips maintained the breeding aggregation.

During the dispersion phase, each female randomly spread her locations inland more and more within the study area, indicating a radical change in the individual spatial behaviour. By interpreting the population level only, the individual females could have randomly spread at different times and then restricted their locations to small areas. Each female also could have spread her locations more and more within the study area. Both these behaviours could have produced the pattern visible at the population level. However, the

Table 3. Univariate GLMs produced for the distances moved by females with two fixed factors: Year (two levels: 2002 and 2003) and Status (two levels: BRA or female whose pup survived, and BRD or female whose pup died during the study) for days before pupping, pupping day and days after pupping (df = 1).

	Year			Status	
	<i>N</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Days before pupping	139	0.016	0.899	0.661	0.418
Pupping day	150	1.743	0.189	6.805	0.010
Days after pupping	148	8.903	0.003	2.811	0.094

Remark: no interaction between the two factors.

investigation at the individual level revealed that the spread of the female population resulted from their choice to move to different locations inland each time they were onshore. At various dates during their dispersion phase, each female left Sandy Bay and took her pup to another site to nurse. By the end of March, the entire female population and their pups had left Sandy Bay. While the individual breeding phase, and resulting formation of a breeding aggregation, is common in pinnipeds, the individual dispersion phase inland seems an unexpected element of the spatial behaviour for pinnipeds.

While all otariids, and many phocids, form temporal breeding aggregations (Boness, 1991), little attention has been paid to the dispersion phase. In Gentry (1998), Northern fur seals, *Callorhinus ursinus*, have maximum distances amongst nursing sites during one year at the breeding colony of 11 m and Steller sea lions, *Eumetopias jubatus*, of around 20 m. In the Galapagos sea lion, *Zalophus wollebaeki*, breeding females have a consistently small home range all year round (Wolf & Trillmich, 2007). Thus, the females of these species do not seem to exhibit a dispersion phase, although the female Galapagos sea lions changed their habitat use after the breeding period ended (Wolf et al., 2005). Female Antarctic fur seals, *Arctocephalus gazella*, however, can have ‘hundreds of meters’ between nursing sites, but this dispersion occurs along the coastline rather than inland (Doidge et al. (1986) cited from Gentry, 1998). In grey seals, *Halichoerus grypus*, Pomeroy et al. (1994) indicated a decrease in the degree of aggregation of females over the breeding season, but no significant changes of nursing locations. Campagna & Le Bœuf (1988) reported that female Southern sea lions, *Otaria flavescens*,

started moving freely and dispersed once adult males left the breeding area. This seems to correspond to a possible dispersion phase but to a lesser extent than in the New Zealand sea lion. It is hard to conclude if the dispersion phase exhibited by the female New Zealand sea lions at Sandy Bay is unusual due to the lack of research in fine-scale spatial terrestrial behaviour for pinnipeds. However, there are only a few reports of individual pinnipeds found more than one hundred meters inland for other species that were better investigated or more traditionally harvested (Evans & Raga, 2001). We expect that, at least the scale of the dispersion phase (with final locations of females and pups almost 800 m from the ocean), is likely unique to the New Zealand sea lion.

The dispersion phase of female New Zealand sea lions may be unusual, but their behaviour within the breeding aggregation does not differ from the typical patterns of pinnipeds. Two main hypotheses can be proposed to explain the dispersion phase by comparing the similarities and differences with other species. Firstly, as reported for the Californian sea lions, *Zalophus californianus* (Peterson & Bartholomew, 1967), the largest adult males leave the breeding area after the last copulations, while sub-adult males stay and gain access to the breeding area. These sub-adult males harass the females to mate, and may seize the pups, but often do not protect females against other males (Wilkinson et al., 2000; personal observation). Young male Southern sea lions also harass females once the largest males leave (Campagna & Le Bœuf, 1988). The benefits of being clustered for females decrease and this should lead to their eventual dispersion because there is no more dilution effect of male harassment.

Secondly, the constant movements of the females to various random locations during the dispersion phase also may be related to the avoidance of parasite-infected zones. Hookworms, *Uncinaria* spp., have been found in New Zealand sea lion adult females (Marlow, 1975) and pups (Castinel et al., 2006). The adult form of this parasite is known to be a significant source of pup mortality in pinnipeds (Olsen & Lyons, 1965; Lyons et al., 1997, 2003). It is typical that greater parasite infection rates causing higher mortality are detected in groups with higher density (e.g., the great tit, *Parus major*, Daan & Tinbergen, 1997). By exhibiting a dispersion phase, female New Zealand sea lions would avoid using areas that have been previously infested by the parasite, at the same time reducing their density and, therefore, limiting the risk of infection. Castinel et al. (2007) also showed that

adult forms of hookworms in the New Zealand sea lion produce eggs to infect new hosts around mid-January which is similar to the mean start of the dispersion phase found in this study (21 January). However, such behaviour as the dispersion phase has never been reported for other species. In the Californian sea lion, the breeding aggregation is at the water's edge within areas washed up by the tide (Peterson & Bartholomew, 1967), hence the occurrence of parasites should be limited by this behaviour. The breeding area of New Zealand sea lions at Sandy Bay is high on the beach and only covered by the tide during large-scale southern storms (personal observation).

During the dispersion phase, females progressively left Sandy Bay with their pups. By the end of March, the female population deserted Sandy Bay. This behaviour is in contrast with the behaviour adopted by the female Australian sea lions, *Neophoca cinerea*, which use the same small island and space as they pup year-round (Gales et al., 1992). The female Galapagos sea lions also keep using the same small areas year round (Wolf & Trillmich, 2007). Californian sea lions were reported as probably staying within the vicinity of the breeding colony year-round with more or less use of the breeding area (Peterson & Bartholomew, 1967). Female Northern fur seals and Steller sea lions however exhibit large-scale movements after the breeding season and the breeding sites are uninhabited, or considerably less used (Gentry, 1998; Raum-Suryan et al., 2004).

These differences are not understood, but are likely related to seasonal prey availability of particular geographical scales. For example, the diet of the New Zealand sea lion was found to vary seasonally (Lalas, 1997). Depending on the distribution of resources at sea, in species where large-scale movements are detected, females with pups may also move to other sites to limit competition amongst pups while they develop their foraging skills. Steller sea lion pups were found to forage near shore during the first year of their lives (Raum-Suryan et al., 2004). Juvenile Australian sea lions also still have limited diving abilities at two-year old which is thought to lessen their available foraging habitat (Fowler et al., 2006). Because of their restricted available foraging areas, competition amongst pups may be more considerable than amongst adults around terrestrial aggregations.

Movements of females and pup survival

The spatial distribution of breeding female New Zealand sea lions' locations did not seem to affect their reproductive success. Pup survival was not affected by the NNIs. However, the movements of female New Zealand sea

lions may affect the pup survival during the day of pupping. The perinatal period is critical for a breeding otariid female as it includes the birth of the pup and also the imprinting, the time during which the female and the pup get familiar before the female leaves for her first foraging trip at sea (Bowen, 1991). In this study, females were sedentary during the day of pupping, with 69% fewer movements than during the days spent ashore prior to birth. Females probably reduced their movements to a minimum on the day of pupping to facilitate contact with their pups (Lawson & Renouf, 1987). The lower variation in distance moved on the day of pupping indicated that all females reduced their movements to a minimum. During the other days, variation amongst individuals was higher and females may not have such a constraint to be sedentary (see Figure 8).

In mammalian species, imprinting between mother and offspring occurs during a 'sensitive period' after birth. Disturbance of the pair during this period may influence the likelihood of survival of the offspring (Lévy et al., 1996). Gisiner & Schusterman (1991) recorded that Californian sea lion mother-pup pairs, with pups aged less than a day, could already acoustically recognise each other. Lawson & Renouf (1987) noted that amongst harbor seals, *Phoca vitulina*, pups were able to orientate towards their mothers within 45 min of birth. The observed higher rate of pup death for females moving more during the pupping day could be due to a weak bond between the female-pup pair following compelled movements of the female during the imprinting period. Unfortunately, the cause of the death of the pups and the females' behaviours were not determined in this study. However, this same hypothesis is supported by McCulloch & Boness (2000) for grey seals. More in-depth studies (especially in time and with determination of the cause of pup death) may reveal further influence of females' movements and locations of nursing sites on pup survival (Pomeroy et al., 2001).

Population size and movement of females

The locations of female New Zealand sea lions in 2002 were overall less aggregated than in 2003 whereas the typical difference in distribution of locations between the breeding phase and the dispersion phase was detected with the same intensity in both years. During the days after pupping of the perinatal period, breeding females also moved greater distances in 2002 than in 2003. In 2003, the number of breeding females at Sandy Bay increased by

21.3% from the number in 2002. Based on Cassini's (2000) model, smaller groups of females have a higher harassment rate by males than larger groups. Although our study is based on two years, we observed that the lower number of females in 2002 have increased the male harassment rate (personal observation). Due to this greater pressure, females were possibly forced to move more to avoid this harassment compared with females in 2003. This hypothesis is also supported by the fact that pup mortality was higher in 2002 (33%) than in 2003 (21%; Chilvers et al., 2007), which may also be due to more male-related pup deaths in a less dense female population (Wilkinson et al., 2000). Because several other factors may lead to pup death, the relationship amongst population size, spatial behaviour and pup survival of the New Zealand sea lion needs further investigation. In several pinniped species, density of the population dictated the movements of breeding females, which, in turn, influenced pup survival (e.g., Southern sea lions, Campagna et al., 1992; grey seals, Boness et al., 1995; elephant seals, Baldi et al., 1996).

Conclusion

Here we present the first quantitative insight into the spatial behaviour of the female New Zealand sea lions in the terrestrial environment. The two phases, breeding and dispersion, and a radical change in spatial behaviour between these phases were the main characteristics revealed. The aggregation during the breeding phase is common for pinnipeds. Within this breeding aggregation, movements of females can affect pup survival on the day of pupping, as previously recorded for other species. During both the breeding and dispersion phases, population size seems to influence female spatial behaviour. This research also highlighted a lack of literature about fine-scale terrestrial spatial behaviour in pinnipeds, which limited comparisons. However, the terrestrial dispersion phase exhibited by female New Zealand sea lions, which results in the female population being spread within a large area, is likely unusual and unique to this species.

Acknowledgements

The authors would like to thank the New Zealand Department of Conservation (DOC) Science and Research Unit, the University of Otago School of Surveying and Information Science Department, DOC Southland for funding or/and permits and general support. Acknowledgements go to the Research and Enterprise Office of the Otago University for an Otago

Postgraduate Publishing Award granted to A.A.A. during the preparation of this paper. We thank everyone who helped during fieldwork and we are grateful to two anonymous reviewers and the editor for their help with the manuscript.

References

- Baldi, R., Campagna, C., Pedraza, S. & Le Bœuf, B.J. (1996). Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. — *Anim. Behav.* 51: 717-724.
- Beyer, H.L. (2004). Citing online sources: Hawth's analysis tools for ArcGIS. — Available from <http://www.spatial ecology.com/htools>
- Boness, D.J. (1991). Determinants of mating systems in the Otariidae. — In: *Behaviour of pinnipeds* (Renouf, D., ed.). Chapman and Hall, Cambridge, p. 1-44.
- Boness, D.J., Bowen, W.D. & Iverson, S.J. (1995). Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? — *Behav. Ecol. Sociobiol.* 36: 1-10.
- Bowen, W.D. (1991). Behavioural ecology of pinniped neonates. — In: *Behaviour of pinnipeds* (Renouf, D., ed.). Chapman and Hall, Cambridge, p. 66-127.
- Campagna, C., Bisioli, C., Quintana, F., Perez, F. & Vila, A. (1992). Group breeding in sea lions: pups survive better in colonies. — *Anim. Behav.* 43: 541-548.
- Campagna, C. & Le Bœuf, B.J. (1988). Reproductive behaviour of Southern sea lions. — *Behaviour* 104: 233-261.
- Cassini, M.H. (2000). A model on female breeding dispersion and the reproductive systems of pinnipeds. — *Behav. Proc.* 51: 93-99.
- Cassini, M.H. & Fernández-Juridic, E. (2003). Costs and benefits of joining South American sea lion breeding groups: testing the assumptions of a model of female breeding dispersion. — *Can. J. Zool.* 81: 1154-1160.
- Castinel, A., Duignan, P.J., Lyons, E.T., Pomroy, W.E., Gibbs, N., López-Villalobos, N., Chilvers, B.L. & Wilkinson, I.S. (2007). Epidemiology of hookworm (*Uncinaria* spp.) infection in New Zealand (Hooker's) sea lion (*Phocarctos hookeri*) pups on Enderby Island, Auckland Islands (New Zealand) during the breeding seasons from 1999/2000 to 2004/2005. — *Parasitol. Res.* 101: 53-62.
- Castinel, A., Duignan, P.J., Pomroy, W.E., Lyons, E.T., Nadler, S.A., Dailey, M.D., Wilkinson, I.S. & Chilvers, B.L. (2006). First report and characterisation of adult *Uncinaria* spp. in New Zealand sea lion (*Phocarctos hookeri*) pups. — *Parasitol. Res.* 98: 304-309.
- Childerhouse, S. & Gales, N.J. (1998). The historic and modern distribution and abundance of the New Zealand sea lion. — *New Zeal. J. Zool.* 25: 1-16.
- Chilvers, B.L., Robertson, B.C., Wilkinson, I.S. & Duignan, P. (2006). Growth and survival of New Zealand sea lions, *Phocarctos hookeri*: birth to 3 months. — *Polar Biol.* 30: 459-469.
- Chilvers, B.L., Robertson, B.C., Wilkinson, I.S., Duignan, P.J. & Gemmill, N.J. (2005). Male harassment of female New Zealand sea lions; mortality, injury and harassment avoidance. — *Can. J. Zool.* 83: 642-648.
- Chilvers, B.L., Wilkinson, I.S. & Childerhouse, S. (2007). New Zealand sea lion, *Phocarctos hookeri*, pup production — 1995 to 2006. — *New Zeal. J. Mar. Fresh.* 41: 205-213.

- Clark, P.J. & Evans, F.C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. — *Ecology* 35: 445-453.
- Daan, S. & Tinbergen, J.M. (1997). Adaptations of life histories. — In: *Behavioural ecology: an evolutionary approach* (Krebs, J.R. & Davies, N.B., eds). Blackwell, Oxford, p. 311-333.
- Eden, A.W. (1955). *Islands of despair*. — Andrew Melrose, London.
- Evans, P.G.H. & Raga, J.A. (2001). *Marine mammal: biology and evolution*. — Kluwer Academic/Plenum, New York, NY.
- Fowler, S.L., Costa, D.P., Arnould, J.P.Y., Gales, N.J. & Kuhn, C.E. (2006). Ontogeny of diving behaviour in the Australian sea lion: trials of adolescence in a late boomer. — *Ecology* 75: 358-367.
- Gales, N.J., Cheal, A.J., Pobar, G.J. & Williamson, P. (1992). Breeding biology and movements of Australian sea lions, *Neophoca cinerea*, off the West coast of Western Australia. — *Wildlife Res.* 19: 405-416.
- Gentry, R.L. (1998). *Behaviour and ecology of the Northern fur seal*. — Princeton University Press, Princeton, NJ.
- Gisiner, R. & Schusterman, R.J. (1991). Californian sea lion pups play an active role in reunions with their mothers. — *Anim. Behav.* 41: 364-366.
- Goodchild, M.F. (1986). *Spatial autocorrelation*. — Geo Bks, Norwich.
- Khaemba, W.M. (2001). Spatial point pattern analysis of aerial surveys data to assess clustering in wildlife distributions. — *Int. J. App. Earth Obs. Geoinf.* 3: 139-145.
- Kirby, D.S. & Abraham, E.R. (2003). Tuna schools/aggregations in surface longline data 1993-1998. — *New Zeal. Mar. Fresh.* 37: 633-644.
- Lalas, C. (1997). Prey of Hooker's sea lions based at Otago Peninsula, New Zealand. — In: *Marine Mammal Research in the southern hemisphere* (Hindell, M. & Kemper, C., eds). Surrey Beatty and Sons, Chipping Norton, NSW, p. 143-150.
- Lawson, J.W. & Renouf, D. (1987). Bonding and weaning in harbor seals, *Phoca vitulina*. — *J. Mammal.* 68: 445-449.
- Lévy, F., Porter, R.H., Kendrick, K.M., Keverne, E.B. & Romeyer, A. (1996). Physiological, sensory and experiential factors of parental care in sheep. — *Adv. Stud. Behav.* 25: 385-422.
- Lyons, E.T., DeLong, R.L., Merlin, S.R. & Tolliver, S.C. (1997). *Uncinariasis* in northern fur seal and California sea lion pups from California. — *J. Wildlife Dis.* 33: 848-852.
- Lyons, E.T., DeLong, R.L., Sparker, T.R., Melin, S.R. & Tolliver, S.C. (2003). Observations in 2001 on hookworms (*Uncinaria spp.*) in otariid pinnipeds. — *Parasitol. Res.* 89: 503-505.
- Mackworth, W.A. & Munce, W.J. (1999). Enderby settlements diaries: records of a British colony at the Auckland Islands 1849-1852. — (Dingwall, P.R., Fraser, C., Gregory, J.C. & Robertson, C.J.R., eds). Wild Press and Wendsell Press, Wellington.
- Marlow, B.J. (1975). The comparative behaviour of the Australasian sea lions *Neophoca cinerea* and *Phocartos hookeri*. — *Mammalia* 39: 159-230.
- McCulloch, S. & Boness, D.J. (2000). Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia. — *Can. J. Zool.* 251: 449-455.
- McNally, N., Heinrich, S. & Childerhouse, S. (2001). Distribution and breeding of New Zealand sea lions on Campbell Island. — *New Zeal. J. Zool.* 28: 79-87.
- Mohr, C.O. (1947). Table of equivalent populations of North American small mammals. — *Am. Midl. Nat.* 37: 223-249.

- Olsen, O.W. & Lyons, E.T. (1965). Life cycle of *Uncinaria lucasi* Stiles, 1901 of fur seals, *Callorhinus ursinus* Linn., on the Pribilof Islands, Alaska. — *J. Parasitol.* 51: 689-700.
- Parrish, J.K. & Edelman-Keshet, L. (1999). Complexity, pattern and evolutionary trade-offs in animal aggregation. — *Science* 284: 99-101.
- Peterson, R.S. & Bartholomew, G.A. (1967). The natural history and behaviour of the Californian sea lion. — The American Society of Mammalogists, Special Publication No. 1. The American Society of Mammalogists, Washington, DC.
- Pomeroy, P.P., Anderson, S.S., Twiss, S.D. & McConnell, B.J. (1994). Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. — *J. Zool.* 233: 429-447.
- Pomeroy, P.P., Worthington, W.J., Amos, W. & Twiss, S.D. (2001). Reproductive performance links to fine-scale spatial patterns of female grey seal relatedness. — *Proc. Roy. Soc. B: Biol.* 268: 711-717.
- Raum-Suryan, K.L., Rehberg, M.J., Pendleton, G.W., Pitcher, K.W. & Gelatt, T.S. (2004). Development of dispersal, movement patterns, and haul-out use by pup and juvenile Steller sea lions in Alaska. — *Mar. Mammal Sci.* 20: 823-850.
- Robertson, B.C., Chilvers, B.L., Duignan, P., Wilkinson, J.S. & Gemmel, N.J. (2006). Dispersal of breeding adult male *Phocarcos hookeri*: implications for disease transmission, population management and species recovery. — *Biol. Conserv.* 127: 227-236.
- Siiter, R.J. (1999). Introduction to animal behaviour. — Brooks/Cole, Pacific Grove, CA.
- Tinbergen, N. (1965). Social behaviour in animals: with special reference to vertebrates. — Methuen, London.
- Trillmich, F. (1990). The behavioural ecology of maternal effort in fur seals and sea lions. — *Behaviour* 114: 3-20.
- Wilkinson, I., Burgess, J. & Cawthorn, M. (2003). New Zealand sea lions and squid: managing fisheries impacts on a threatened marine mammal. — In: *Marine mammals, fisheries, tourism and management issues* (Gales, N., Hindell, M. and Kirkwood, R., eds). CSIRO, Collingwood, VIC, p. 192-207.
- Wilkinson, I.S., Childerhouse, S., Duignan, P.J. & Gulland, F.M.D. (2000). Infanticide and cannibalism in the New Zealand sea lion. — *Mar. Mammal Sci.* 16: 495-500.
- Wilkinson, I.S., Duignan, P.J., Bradshaw, C.J.A. & Chilvers, B.L. (in press). An evaluation of hot-iron branding as a permanent marking method for adult female New Zealand sea lions, *Phocarcos hookeri*. — *Wildlife Res.*
- Wolf, J.B.W., Kauermann, G. & Trillmich, F. (2005). Males in the shade: habitat use and sexual segregation in the Galapagos sea lion (*Zalophus californianus wollebaeki*). — *Behav. Ecol. Sociobiol.* 59: 293-302.
- Wolf, J.B.W. & Trillmich, F. (2007). Beyond habitat requirements: individual fine-scale site fidelity in a colony of the Galapagos sea lion (*Zalophus wollebaeki*) creates conditions for social structuring. — *Oecologia* 152: 553-567.
-