

Seasonal occurrence and diet of leopard seals (*Hydrurga leptonyx*) at Bird Island, South Georgia

T.R. WALKER, I.L. BOYD*, D.J. McCafferty, N. HUIN, R.I. TAYLOR and K. REID

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK
*corresponding author

Abstract: Seasonal haul-out patterns and diet of individually marked leopard seals (*Hydrurga leptonyx*) were investigated at Bird Island, South Georgia during the 1983–96 winters. A total of 2956 leopard seal sightings were made, and 121 seals were tagged during the study, mainly between 1993 and 1996. Photographs of scars and pelage patterns were also used to identify a subset of these individuals across years, which provided no evidence of tag loss between or within years. Leopard seals were observed between April and November; the mean time between the first and last sightings in each year was 208 d (s.d. ± 48). Between 1993–96, eight seals were resident around the island for more than 100 d, and the longest recorded residence was 130 d. The proportion of tagged seals resighted was 0.35 and 0.17 in 1995 and 1996 respectively. Based on estimates of body length, <5% of the seals were juveniles (0–1 years) and >70% were not sexually mature. There was considerable inter-annual variation in abundance, with a maximum of 502 sightings during 1994, compared with a minimum of 21 during 1986 and 1989. Antarctic fur seals (*Arctocephalus gazella*) were the main prey item (58% of kills observed and 53% of scats). Other items included penguins (28% of kills observed and 20% of scats) and fish (24% of scats). Antarctic krill (*Euphausia superba*), southern elephant seals (*Mirounga leonina*) and seabirds other than penguins were also present in the diet in small quantities.

Received 24 April 1997, accepted 27 October 1997

Key words: abundance, diet, fur seal, leopard seal, penguin, predation, seasonality, South Georgia

Introduction

The leopard seal (*Hydrurga leptonyx* de Blainville) is one of the most widespread of the Antarctic seals and has a reputation as a powerful, and potentially significant predator of seabirds and other seals. Despite this, little is known about its general ecology. The leopard seal has a circumpolar distribution occurring primarily throughout Antarctic pack ice during the breeding season, from November to late December (Laws 1984, Siniff & Stone 1985). There appears to be a seasonal dispersal northwards to subantarctic islands during the winter (Gwynn 1953, Rounsevell & Eberhard 1980, Borsa 1990), although small numbers have been observed throughout the year at Iles Kerguelen (Bester 1981, Bester & Roux 1986) and Heard Island (Gwynn 1953, Brown 1957).

The diet of the leopard seal in the pack ice is reported to consist of diverse prey items which most commonly include other seals, such as crabeater seals (Gilbert & Erikson 1977, Øritsland 1977, Siniff *et al.* 1979), fish (Green & Williams 1986), cephalopods (Siniff & Stone 1985) and krill (Lowry *et al.* 1988). The predatory behaviour of leopard seals at penguin colonies has been well documented (Penney & Lowry 1967, Hunt 1973, Müller-Schwarze & Müller-Schwarze 1975, Siniff & Stone 1985, Bester & Roux 1986, Borsa 1990, Kooyman *et al.* 1990, Rogers & Bryden 1995) but little is known of the diet and hunting techniques in other areas, although there is evidence for spatial and temporal variation in the relative proportions of the various prey items

(Laws 1984).

South Georgia (54°59'S, 36°25'W) lies 200–300 km south of the Antarctic Polar Front but usually remains free of pack ice during winter. Leopard seals were first observed during the southern winter at South Georgia during the height of the whaling industry (Matthews 1929). Since 1983, observations have been made of leopard seals by the staff of the British Antarctic Survey station at Bird Island (54°00'S, 38°02'W).

Intensive tagging was initiated at Bird Island during winter 1993 and continued throughout the 1994, 1995 and 1996 winters. This study was established to help interpret interannual variability in the number of leopard seals observed at Bird Island and it addressed three main questions;

- 1) do leopard seals return to forage at the same sites in consecutive years;
- 2) what is the rate of turnover of individuals in the population, and
- 3) what is the main prey of these leopard seals?

Methods

Seasonal haulout and interannual variability

Leopard seals were counted daily on beaches within the region of Bird Island known as Jordan Cove (Landing Beach, Freshwater Beach and Main Bay) from April through to

November during the 1994–96 winters. These beach sites have been described previously (Boyd 1989). Approximately once per week leopard seals were counted on the remaining beaches of the island (Everman Cove and Johnson Beach).

Total numbers of leopard seal sightings for Freshwater Beach were also available each year from 1983–93. Probable inter-annual variation in observer effort was reduced by using only those sightings made at Freshwater Beach, the location of the research station. A standard system of recording all leopard seal sightings was used: any leopard seal that was on land or feeding at Freshwater Beach was recorded with the date of observation, the detailed location on the beach and the name of the observer. Records were made on a daily basis to eliminate multiple records for an individual seal on the same day. Once leopard seals move on to land they tend to remain in a single location for periods of hours and they do not tend to return to land again on the same day once they have re-entered the water.

Before 1993 photographs were the only method used to help identify individual seals across years. Tagging (Dalton Jumbotags, Dalton Supplies Ltd., UK) took place during 1993–96. Each tag was stamped with an identifying number and the message, 'Inform British Antarctic Survey'. All seals were tagged in the interdigital membrane of the hind flippers. Where possible individual seals were double tagged (one tag in each of the hind flippers). Double tagging was only possible when an individual was found asleep a second time. In addition, and where possible, leopard seals on beaches were also photographed for identification by pelage patterns and scars. This was to help calculate any possible tag loss rates within and across years. Total straight line length was measured (from nose to tip of hind flipper) in those seals that were asleep in an appropriate posture (i.e. stretched out straight). Standard length (nose to tail) was derived by multiplying this total body length by 0.89 (Laws 1957). Those seals that could not be tagged when first sighted were marked with gloss paint. Paint marks remained visible for at least one month after application, allowing seals to be identified later if subsequently tagged. Incidental resights of painted and tagged individuals were made in addition to those during the daily count.

A single leopard seal was tagged ("Allflex" medium sheep tags, Delta Plastics Ltd., New Zealand) in 1988. Others ($n = 14$) were photographed between 1984 and 1993.

Diet and predation

During the 1994 and 1995 winters, scats were collected from known individual seals that had been seen defaecating. Scats were analysed as described by Reid (1995). Leopard seals preying on seabirds and mammals were observed opportunistically during daily rounds of the study area and activities around the research station.

Results

Tag loss

Of five leopard seals double tagged during winter 1994, two were re-sighted during the 1995 winter season and both had retained both their tags. In addition, 12 tagged seals identified, using distinguishing scars and pelage patterns, from photographs taken in 1994 and matched in a blind trial including all photographs of seals taken in 1995, had also retained their tags. This information suggests that tag loss was low enough to be insignificant in this study.

Seasonal haulout and interannual variability in numbers

A total of 2956 leopard seal sightings was made at Freshwater Beach between April 1983 and November 1996 (Table I). One hundred and forty-six seals were tagged. Individuals were observed when lying on beaches, ice floes and icebergs or when in the water, swimming, sleeping or hunting. The ease with which it was possible to read tag numbers depended on the location of the observation but, in general, only when animals were asleep on the beaches could the numbers be read reliably. Many individuals were observed sleeping in the middle of kelp beds with their heads clear of the water. Other sightings included groups of 2–3, but occasionally up to 7 leopard seals, apparently involved in copulations. Winter sightings usually began in April, peaked in August, declined through October and ended in November (Table I). Early sightings in January and February usually occurred at the large macaroni penguin colonies around the island. The mean duration of the season of presence of leopard seals at Bird Island was 208 d ($s d \pm 48$). The index of abundance, based on the total number of leopard seal days per month at Freshwater Beach, between 1983 and 1996 showed a high

Table I. Frequency of occurrence (expressed as the total number of leopard seal days recorded) and duration (time from first to last sighting each year) of leopard seals at Bird Island, South Georgia, 1982–96.

Year	Frequency	Duration (days)	First sighting	Last sighting
1982	–	199	20 Apr	05 Nov
1983	40	222	07 Apr	15 Nov
1984	90	143	08 May	28 Oct
1985	37	254	10 Apr	20 Dec
1986	21	313	02 Jan	11 Nov
1987	454	187	01 May	03 Nov
1988	259	133	20 May	11 Nov
1989	21	290	13 Feb	30 Nov
1990	127	177	25 May	18 Nov
1991	166	202	24 May	12 Dec
1992	298	192	27 Apr	04 Nov
1993	54	181	27 Apr	24 Oct
1994	502	219	29 Apr	04 Dec
1995	428	197	05 May	17 Nov
1996	459	205	22 Apr	13 Nov
Mean \pm s d	211 \pm 184	208 \pm 48	18 Apr \pm 39d	16 Nov \pm 17d

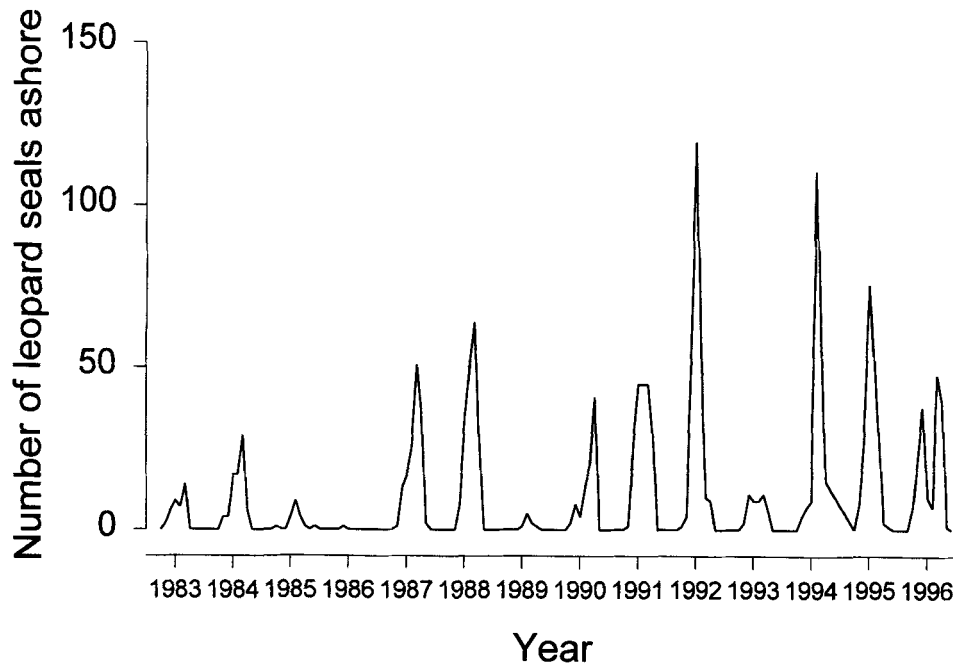


Fig. 1. Numbers of leopard seals observed at Freshwater Beach, Bird Island, South Georgia. Observations are expressed as the total number of leopard seal days each month between 1983–96.

degree of seasonal and inter-annual variation in the absolute numbers of seals sighted (Fig. 1). However, there was a significant trend showing an apparent increase in the numbers of seals sighted through the period of observation (ANOVA, $F_{1,12} = 7.77$, $P < 0.02$).

The pattern of presence and absence of tagged leopard seals in the study area over three seasons from 1994–96 (Fig. 2) shows that they arrived throughout the period from May through September and that many of those arriving early were present at Bird Island into late September and October. However, there were differences between years. In 1994, arrivals appeared to be later than in the subsequent years and in 1996 few of the seals that arrived early were observed after July. Also in 1996, few new seals were observed during July and August but there was an increase in new arrivals during September and October.

Of the 153 leopard seals tagged or photographed, 129 were tagged and 24 were identified only from photographs. Photographs were only used as the sole form of identification for leopard seals seen before 1993. Forty four were not seen again at Bird Island after the first recorded day of residence and a further 27 were seen only once after tagging. Thirty four seals stayed at the island for more than 50 d, and eight stayed for more than 100 d (Table II). The longest recorded residence was 150 d. This seal was resighted six times between 21 May and its last sighting on 28 September 1996, and it was also present in three consecutive years.

Tag resighting between years

Fourteen leopard seals were resighted in years subsequent to tagging. One seal with a white Allflex tag, which had been deployed in 1988, was resighted once in 1990 and four times in 1996. Eight seals were present through three consecutive

seasons. These seals were often seen ashore on the same beach sites at which they were tagged (Fig. 3). Not only was there a tendency for seals to be observed on the same beaches, but the same specific locations upon those beaches also tended to be used.

Only four tags were applied in 1993 and one of these individuals was resighted in 1994. Of the 42 individuals tagged during 1994, 11 were seen at Bird Island in 1995, which represents a 26% recovery rate. Eight of these individuals were then resighted again in 1996 when another individual that had been tagged in 1994 but not seen in 1995 was also resighted. Of 31 seals tagged in 1995, only one was resighted in 1996. A further 53 tags were applied in 1996. These data show that most resightings were of seals tagged in 1994. This is probably because a small group of individuals, representing about one-third to one-fifth of the population in any one year, may be considered to be resident animals in the sense that they tend to return to the same locations in consecutive years.

Table II. Durations of residence for individual leopard seals either known from photographs or tagged at Bird Island, South Georgia, 1984–96.

Residence (days)	Number of leopard seals								Total
	1984	1985	1987	1988	1993	1994	1995	1996	
1	–	1	–	–	2	17	9	15	44
2	–	–	–	–	–	5	2	8	15
3–9	–	–	–	1	–	1	3	6	11
10–19	–	–	–	–	–	2	1	5	8
20–29	–	–	3	1	1	1	2	5	13
30–49	1	–	–	1	–	8	3	15	28
50–99	2	–	1	–	1	8	8	6	26
>100	–	–	–	–	–	2	3	3	8
Total	3	1	4	3	4	44	31	55	153

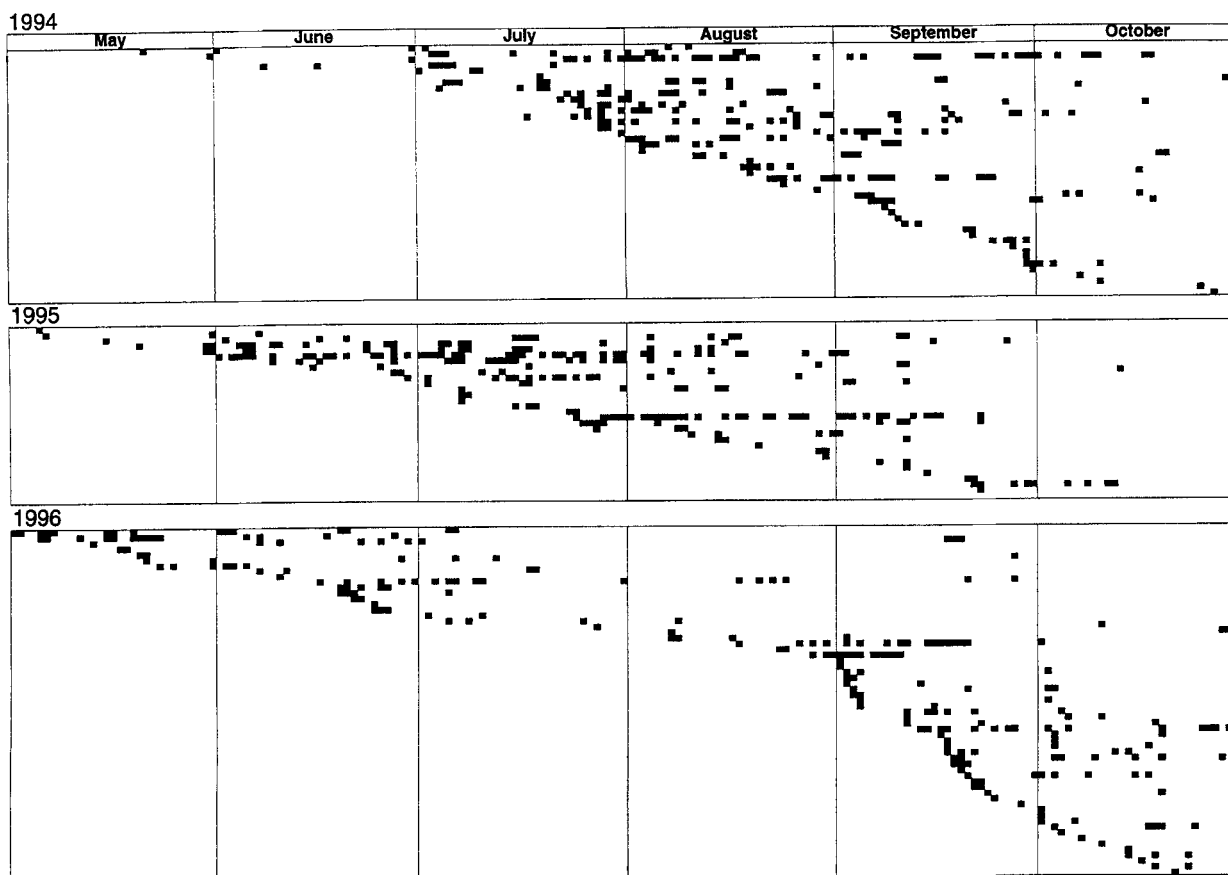


Fig. 2. Patterns of presence and absence of leopard seals tagged at Bird Island, South Georgia during 1994–96. Each row represents an individual leopard seal; blanked off regions show the period when the leopard seal was observed ashore.

One tagged individual was resighted at Seal Island, South Shetland Islands (60°59'S 55°23'W) on 18 Jan 1995 (Lisa Hiruki, personal communication). This animal had been tagged on 7 October 1994 and had therefore taken approximately three months to cover a minimum distance of 1300 km from Bird Island. This individual was only ever seen on the day of tagging at Bird Island.

Age and sex classes observed

Leopard seals measured during the study, were allocated, based on their lengths, to the age and sex classes shown in Table III. Seals of adult size (>4 years) accounted for 20–25% of the population with the remainder being immatures although less than 5% were classified as <1 year old. Males

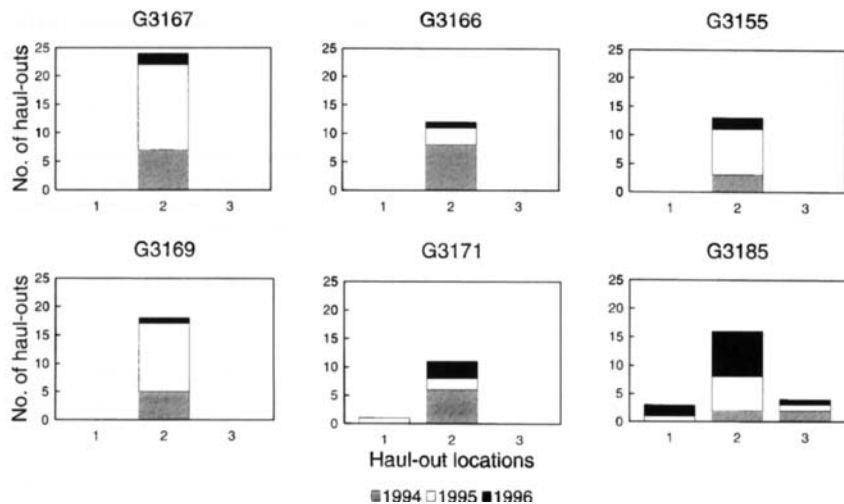


Fig. 3. Locations of six leopard seals originally tagged at Freshwater Beach, Bird Island, South Georgia, obtained from observations between 10.00–12.00 and 18.00–20.00 daily. Seals tended to come ashore at specific locations upon the same beaches. All beaches were within a 3 km stretch of coastline.

Key to locations

- 1 Main Bay
- 2 Freshwater Beach
- 3 Landing Beach

Table III. Age and sex composition of leopard seals at Bird Island, South Georgia. Ages were estimated from standard length using the method described by Laws (1957). Results are given for all marked seals where lengths were recorded.

Year	n	Males (%)	Females (%)	Estimate age (years)				
				0-1 Juv (%)	1-2 Imm (%)	2-3 Imm (%)	3-4 Imm (%)	>4 Adult (%)
1994	39	59	41	4.5	40.0	31.0	0	24.5
1995	26	54	46	3.2	26.0	19.3	32.3	19.3
1996	51	67	33	-	-	-	-	-

were present in greater numbers each year than females (Table III) and they also arrived earlier in the winter than females (Fig. 4). Ten individuals measured in successive years (1994 and 1995) showed no significant increase in length between years (one way ANOVA $F_{1,9} = 0.22 P > 0.6$). Overall, leopard seals appeared to be in good condition and one individual (mass 155 kg), which died of an unknown cause, had a sternal blubber depth of 4.5 cm and a total blubber content of 35% of body mass based on the formula of Ryg *et al.* (1990).

Diet and predation

Direct observation of predation by leopard seals at Bird Island showed that kills invariably occurred in the water and Antarctic fur seals accounted for most of the observed kills (Table IV). Gentoo penguins were the next most commonly observed item in the leopard seal diet during the winter months and macaroni penguins were eaten by leopard seals during the summer.

The prey components contained in scats collected from leopard seals at Bird Island ($n = 45$) showed that more than half (53.3%) contained the remains of juvenile Antarctic fur seals (Table V). The proportions of fish and penguin remains in the scats were similar, comprising only one quarter and one fifth of all scats sorted, respectively. Only one scat contained krill, but this was after large quantities were seen washed up on the beaches around Bird Island. Five scats were collected from one female leopard seal and all of these contained only fur seal hair.

Table V. Frequency of occurrence of prey items from scats ($n = 45$) of tagged leopard seals during 1994 and 1995.

Year	Prey items			
	fur seal hair	penguin feathers	krill	fish
1994	5	5	0	5
1995	19	4	1	6
Total (%)	24 (53)	9 (20)	1 (2)	11 (24)

Table IV. Number and proportion of prey items ($n = 162$) taken by leopard seals at Bird Island, South Georgia, 1983-95.

Prey item	n	%
Antarctic fur seal (sub-adult) (<i>Arctocephalus gazella</i>)	94	58.0
Elephant seal (<i>Mirounga leonina</i>)*	5	3.0
Gentoo penguin (<i>Pygoscelis papua</i>)	14	8.6
Macaroni penguin (<i>Eudyptes chrysolophus</i>)	45	28.0
Diving petrel (<i>Pelecanoides sp.</i>)	3	1.9
Cape petrel (<i>Daption capense</i>)	1	0.6

* all observations were of small (c. 1.5-2.0 m) elephant seals.

Discussion

Seasonal abundance

As at other subantarctic sites (Rounsevell & Eberhard 1980, Borsa 1990), there was a seasonal pattern of abundance with sightings throughout the winter, usually peaking in August or September, and animals generally being absent from late spring to mid-autumn. While this pattern was consistent between years, there was large inter-annual variation in the numbers of seals sighted. The measure of leopard seal abundance did not take into account multiple sightings of the same individual on different days so it could have been influenced by small numbers of individuals taking up residence at Bird Island. Therefore the total number of leopard seal days observed in each month (Fig. 1) will not provide a true representation of variations in the total numbers of leopard seals present at Bird Island. Similar interannual variability has been observed at Macquarie Island and a 4-5 year periodicity has been suggested (Rounsevell 1988, Testa *et al.* 1991). Temporal overlap between the Macquarie Island and Bird Island data sets is insufficient to examine the possibility that changes at these sites are in phase but the

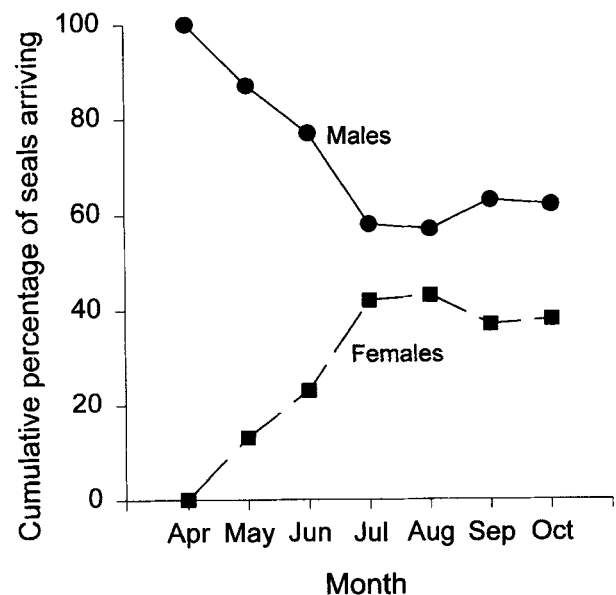


Fig. 4. Percentages of male and female leopard seals arriving at Bird Island, South Georgia, by month, between 1994-96.

periodicity of change at Bird Island appears to be 3–4 years, based on the two complete cycles observed to date.

There was an apparent increase in the abundance of leopard seals at Bird Island since 1983. Although efforts were made both in the field and during analysis to standardize the observer effort across the whole of the study period, it remains possible that this increase was caused by increased observer effort as the study progressed. However, it is also possible that it may signal an increasing population in the region, possibly attracted by increasingly abundant fur seal prey (Boyd 1993).

Population structure

Based on measurements of body length most of the leopard seals hauling out at Bird Island were immature. One-third to one-fifth of seals returned in successive years and the observation that these individuals did not show any significant increment in length between years suggests that they were mainly adult seals. The high frequency of immatures also concurs with the observations of leopard seals at Macquarie Island (Rounsevell 1988) but this is the first example of long-term site fidelity in leopard seals. It appears that the winter leopard seal population at Bird Island is composed of a small group (10–15) of individuals that return annually, another larger group that may remain within the region for a period of 1–3 months within a season and a still larger group that appears to be present for periods of <10 days and that were never seen again (Table II). In addition, those seals that were resident at Bird Island tended to use specific locations for hauling out.

Foraging behaviour, diet and movements

The observations of diet and predation are likely to have been biased towards those individuals that were resident at Bird Island and they suggest strongly that these animals were attracted to this location because of the availability of seals and penguins throughout the winter. Past observations at South Georgia, Iles Kerguelen and Heard Island have also suggested the importance of Antarctic fur seals in the diet of leopard seals (McCann & Doidge 1987, Borsa 1990, Shaughnessy *et al.* 1998). However, the diet observed in this study may not reflect the diet of leopard seals in general. It is possible that the current observations are of a small group of leopard seals which exploit a specialist niche. This is supported by the presence of one leopard seal, that had been tagged at Bird Island, at a fur seal colony in the region of the Antarctic Peninsula. Past observations of leopard seal diets suggest that the principal components are fish (Green & Williams 1986) and krill (Lowry *et al.* 1988).

The relatively small number of juvenile (0–1 year old) leopard seals observed at Bird Island suggests that these individuals do not tend to exploit large vertebrate prey like seals and penguins (see also Siniff & Bengtson 1977). Young

leopard seals may not have sufficient ability to exploit such a prey resource or they may be excluded from such prey by competition with adult leopard seals for the most profitable feeding locations. However, there was insufficient data matching observations of predation on prey of different sizes and the sex or age class of leopard seals in this study to allow comparison of diets between different classes of individuals.

Gilbert & Erickson (1977) suggested that northward dispersal of non-breeding individuals may occur in winter due to intraspecific competition for food or because of limited access to food in the winter sea ice. Furthermore, based on surveys of leopard seals in pack ice, Rogers & Bryden (1997) suggested that competition for space could influence the dispersion. The results of this study showing that specific individuals tend to occupy specific areas support the view that leopard seals may compete for access to prime habitat, such as around fur seal and penguin colonies (Bester & Roux 1986, Borsa 1990).

The sex ratio was biased in favour of males during the early part of the winter. This suggests that males may move north out of the pack ice before females. The general bias in sex ratio could represent a bias within the population as a whole but it is more likely to reflect different diet selectivity by the sexes and suggests that males may be more likely to take large vertebrate prey. The movement of seals away from Bird Island in October coincides with the beginning of the recession of the pack ice and the assumed breeding season for leopard seals (Siniff & Stone 1985). Therefore, seals may move south in October to breed and because they will then have access to additional feeding areas as the sea ice begins to break up and recede. Only one record, from September 1987, exists of a leopard seal birth at Bird Island, while none has been reported at Macquarie Island (Rounsevell & Eberhard 1980).

This study has confirmed that leopard seals take a wide variety of prey, including young elephant seals (see also Gwynn 1953, Siniff & Bengtson 1977, Borsa 1990). The fish remains observed in leopard seal scats collected at Bird Island must be interpreted with caution as these remains may have derived from the gut of mammalian or avian prey since fish are known to be important in the winter diet of Antarctic fur seals (Reid 1995) and gentoo penguins (Williams 1991).

Conclusions

These results have shown that the abundance of leopard seals at Bird Island varies seasonally and between years, possibly in a 3–4 year cycle. Small numbers of individual animals show fidelity with and between years to specific locations for hauling out and also probably for feeding. These individuals appear to feed mainly on seals and penguins, at least through the winter period. Leopard seal numbers at Bird Island may have increased since the study began in 1983.

Acknowledgements

We especially thank all the past overwintering staff at the British Antarctic Survey base on Bird Island for recording leopard seal sightings. In particular, we thank Dr N. Cobley, Richard Humpidge and Dr S. Berrow for spending countless hours in the field helping with tagging and resights and for constructive comments on the manuscript. We thank Dr P.L. Boveng, Lisa Hiruki and the other US researchers on Seal Island, Antarctica for passing on details of a resighting during 1995. We are grateful to Dr M.N. Bester, Dr P.L. Boveng and Dr P.D. Shaughnessy for commenting on the manuscript.

References

- BESTER, M.N. 1981. Fur seals *Arctocephalus gazella* and leopard seals *Hydrurga leptonyx* at the Courbet Peninsula, Kerguelen. *South African Journal of Antarctic Research*, **10/11**, 35-38.
- BESTER, M.N. & ROUX, J-P. 1986. Summer presence of leopard seals (*Hydrurga leptonyx*) at the Courbet Peninsula, Iles Kerguelen. *South African Journal of Antarctic Research*, **16**, 29-32.
- BORSA, P. 1990. Seasonal occurrence of the leopard seal (*Hydrurga leptonyx*) in the Kerguelen Islands. *Canadian Journal of Zoology*, **68**, 405-408.
- BOYD, I.L. 1989. Spatial and temporal distribution of Antarctic fur seals (*Arctocephalus gazella*) on the breeding grounds at Bird Island, South Georgia. *Polar Biology*, **10**, 179-185.
- BOYD, I.L. 1993. Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Science*, **5**, 17-24.
- BROWN, K.G. 1957. The leopard seal at Heard Island, 1951-54. *ANARE Interim Report*, **16**, 1-34.
- GREEN, K. & WILLIAMS, R. 1986. Observations on food remains in faeces of elephant, leopard and crabeater seals. *Polar Biology*, **6**, 43-45.
- GILBERT, J.R. & ERIKSON, A.W. 1977. Distribution and abundance of seals in the pack ice of the Pacific Sector of the Southern Ocean. In LLANO, G.A., ed. *Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 703-740.
- GWYNN, A.M. 1953. The status of the leopard seal at Heard Island and Macquarie Island, 1948-1950. *ANARE Interim Reports*, **3**, 1-33.
- HUNT, J.F. 1973. Observations on the seals of Elephant Island, South Shetland Islands, 1970-71. *British Antarctic Survey Bulletin*, No. 36, 99-104.
- KOORYMAN, G.L., CROLL, D., STONE, S. & SMITH, S. 1990. Emperor penguin colony at Cape Washington, Antarctica. *Polar Record*, **26**, 103-108.
- LAWS, R.M. 1957. On the growth rates of the leopard seal, *Hydrurga leptonyx* (De Blainville, 1820). *Säugetierkundliche Mitteilungen*, **5**, 49-55.
- LAWS, R.M. 1984. Seals. In LAWS, R.M., ed. *Antarctic ecology*. Vol. II. London: Academic Press, 621-715.
- LOWRY, L.F., TESTA, J.W. & CALVERT, W. 1988. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. *Polar Biology*, **8**, 475-478.
- MCCANN, T.S. & DOIDGE, D.W. 1987. Antarctic fur seal, *Arctocephalus gazella*. In CROXALL, J.P. & GENTRY, R.L., eds. *Status, biology, and ecology of fur seals*. NOAA Technical Report NMFS, No. 51, 5-8.
- MATTHEWS, L.H. 1929. The natural history of the elephant seal with notes on other seals found at South Georgia. *Discovery Reports*, **1**, 233-256.
- MÜLLER-SCHWARZE, D. & MÜLLER-SCHWARZE, C. 1975. Relations between leopard seals and Adélie penguins. *Rapports et Proces-Verbaux des Reunions du Conseil Permanent International pour l'Exploration de la Mer*, **169**, 394-404.
- ØRITSLAND, T. 1977. Food consumption of seals in the Antarctic pack ice. In LLANO, G.A., ed. *Adaptations within Antarctic ecosystems*. Washington, DC: Smithsonian Institution, 749-768.
- PENNEY, R.L. & LOWRY, G. 1967. Leopard seal predation on Adélie penguins. *Ecology*, **48**, 879-881.
- REID, K. 1995. The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarctic Science*, **7**, 241-249.
- ROGERS, T.L. & BRYDEN, M.M. 1995. Predation of Adélie penguins (*Pygoscelis adeliae*) by leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. *Canadian Journal of Zoology*, **73**, 1001-1004.
- ROGERS, T.L. & BRYDEN, M.M. 1997. Density and haul-out behavior of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. *Marine Mammal Science*, **13**, 293-302.
- ROUNSEVELL, D. 1988. Periodic irruptions of itinerant leopard seals within the Australian sector of the Southern Ocean, 1976-86. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 189-191.
- ROUNSEVELL, D. & EBERHARD, I. 1980. Leopard seals, *Hydrurga leptonyx* (Pinnipedia), at Macquarie Island from 1949 to 1979. *Australian Wildlife Research*, **7**, 403-415.
- RYG, M., LYDERSEN, C., MARKUSSEN, N.H., SMITH, T.G. & ØRITSLAND, N.A. 1990. Estimating the blubber content of phocid seals. *Canadian Journal of Fisheries and Aquatic Science*, **47**, 1223-1227.
- SHAUGHNESSY, P.D., ERB, E. & GREEN, K. 1998. Continuing increase in the population size of the Antarctic fur seal *Arctocephalus gazella* at Heard Island, Southern Ocean. *Marine Mammal Science*, **14**, in press.
- SINIFF, D.B. & BENGTON, J.L. 1977. Observations and hypotheses concerning the interactions among crabeater seals, leopard seals, and killer whales. *Journal of Mammology*, **58**, 414-416.
- SINIFF, D.B., STIRLING, I., BENGTON, J.L. & REICHEL, R.A. 1979. Social and reproductive behaviour of crabeater seals (*Lobodon carcinophagus*) during the austral spring. *Canadian Journal of Zoology*, **57**, 2243-2255.
- SINIFF, D.B. & STONE, S. 1985. The role of the leopard seal in the trophodynamics of the Antarctic marine ecosystem. In STEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., eds. *Antarctic nutrient cycles and food webs*. Berlin: Springer-Verlag, 555-560.
- TESTA, J.W., OEHLERT, G., AINLEY, D.G., BENGTON, J.L., SINIFF, D.B., LAWS, R.M. & ROUNSEVELL, D. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 631-639.
- WILLIAMS, T.D. 1991. Foraging ecology and diet of gentoo penguin *Pygoscelis papua* at South Georgia during winter and an assessment of their winter prey consumption. *Ibis*, **133**, 3-13.