

FORAGING RANGE OF THE YELLOW-EYED PENGUIN *MEGADYPTES ANTIPODES*

P.J. MOORE

Science & Research Unit, Department of Conservation, PO Box 10-420, Wellington, New Zealand
(pmoore@doc.govt.nz)

SUMMARY

MOORE, P.J. 1999. Foraging range of the Yellow-eyed Penguin *Megadyptes antipodes*. *Marine Ornithology* 27: 49–58.

Foraging ranges of Yellow-eyed Penguins *Megadyptes antipodes* were estimated off the south-east coast of the South Island, New Zealand during three breeding seasons, 1990/91, 1991/92 and 1992/93. Transmitters were glued to penguins and their foraging locations were estimated by triangulation of radio bearings to two land-based receiving stations. At the main study area – Boulder Beach on the Otago Peninsula – 14 penguins were radio-tracked for two- to three-week periods during three stages of the breeding seasons. Birds at Otago Peninsula foraged over the continental shelf, which is mostly 40–80 m deep and 30 km wide. Foraging time was also measured using dive recorders during the 1993/94 and 1994/95 breeding seasons. The median foraging trip over the five years that recordings were made was 14 hours (range two hours to seven days) and birds travelled a median of 13 km (up to 57 km) from the breeding area. The longer, more distant trips took place during the incubation period, except during 1992/93, when trips were of relatively shorter duration and distance. Failed breeders and nonbreeders travelled farther (females) and for longer (especially males) than breeding birds. Breeding birds that later failed took longer trips during incubation than successful breeders, and females of the former category also travelled farther. Foraging patterns during the postguard period at Long Point were similar to Boulder Beach, although foraging trips were shorter as some birds went to sea two–three times per day. Individuals showed different, although usually overlapping, foraging ranges and retained these patterns at different times of the breeding season and in different years. Some birds were markedly inshore feeders, with centres of activity <5 km from the coast. The majority of birds were midshelf foragers (5–16 km from the coast), while some centred their activity >16 km from the coast. Breeding success, and possibly foraging time and range was affected by disturbance. Breeding success of birds carrying packages and diet sampled was lower than average, but not as low as birds that were diet sampled only.

INTRODUCTION

The Yellow-eyed Penguin *Megadyptes antipodes* is found only in the New Zealand region and is one of the world's rarest penguin species, with a total population of about 1400–2100 pairs (Marchant & Higgins 1990, Moore 1992). During the 1980s and early 1990s there were several decreases in numbers of birds nesting on the South Island, followed by (at least partial) recoveries. Numbers of nests fluctuated between an estimated 600 in 1985 (Darby & Seddon 1990) and 320 in 1989 (Marchant & Higgins 1990). In early 1990 about 150 adults died mysteriously around Otago Peninsula (Gill & Darby 1993), and large numbers of orphaned chicks were reared in captivity and then released. Although this event may have been caused or exacerbated by avian malaria (Graczik *et al.* 1995) or toxins (Gill & Darby 1993), other years of poor survival of adults or chicks were believed to have been caused by food supply changes or shortages (Richdale 1957, van Heezik & Davis 1990, van Heezik 1990). These were probably driven by La Niña/warm water events which were detrimental to the Yellow-eyed Penguin food chain (Moore & Wakelin 1997). There was concern that the frequency of these poor seasons was increasing during the 1980s (van Heezik 1990), and that the Yellow-eyed Penguin had become endangered on the South Island (Marchant & Higgins 1990).

During the die-off of adult penguins in 1990, it was clear that little was known about how Yellow-eyed Penguins were interacting with the marine environment. Most of our insight came from a study of diet during the mid-1980s which suggested that Yellow-eyed Penguins foraged over the continental shelf, mainly in the upper part of the water column (but also at the sea floor), for a limited number of key prey (van Heezik 1990). Changes in diet composition were thought to influence breeding success (van Heezik 1990). A study of dive depth, using capillary tubes, suggested that because the majority of dives were 30–40 m deep, the foraging range would be 7–13 km offshore from Boulder Beach (Seddon & van Heezik 1990). However, this was based on a misinterpretation of the fathom scale of a bathymetry map (Brodie 1967) as metres (Fig. 1 in Seddon & van Heezik 1990), whereas the 30–40 m isobaths lie 1.5–2 km offshore (Carter 1986).

A foraging study was conducted from 1991–1995 to investigate Yellow-eyed Penguin foraging range, dive depth and diet. Preliminary results (Moore *et al.* 1995) and diet (Moore & Wakelin 1997) have been reported on, and foraging range is the subject of this paper. It was hoped to determine what parts of the ocean were important to Yellow-eyed Penguins and whether foraging patterns changed in years of poor survival of adults or chicks.

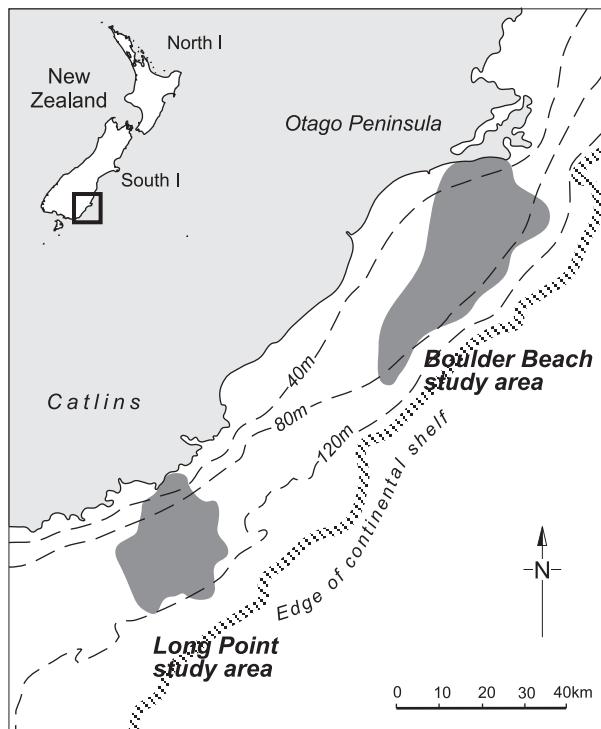


Fig. 1. Yellow-eyed Penguin foraging range study areas at Boulder Beach (Otago Peninsula) and Long Point (Catlins) on the South Island of New Zealand. Approximate bathymetry of the continental shelf is shown and shaded areas indicate those areas used by penguins.

METHODS

The foraging ranges of Yellow-eyed Penguins were studied by attaching transmitters to birds and using land-based radio tracking stations to plot their movements at sea.

The main study area was the A1-Highcliff area (*c.* 40 nests) of Boulder Beach at Otago Peninsula ($45^{\circ}54'S$, $170^{\circ}36'E$; henceforth referred to as Boulder Beach), and additional data were collected at one part of Long Point ($46^{\circ}35'S$, $169^{\circ}35'E$; *c.* 10 nests) in the Catlins, 110 km from Boulder Beach on the southeast coast of New Zealand's South Island (Fig. 1). These breeding sites are in formerly grazed (by domestic stock) areas of coastal scrub and grassland habitat. Offshore bathymetry differs at the two areas (Fig. 1, Carter 1986, Hughes 1987). Although the edge of the continental shelf is a similar distance offshore (about 35 km), the flattest part of the shelf is shallower at Boulder Beach (40–90 m) than at Long Point (80–130 m).

Penguins at Boulder Beach were radio-tracked for two- to three-week periods over three years (26 January–8 February 1991, 9–31 October 1991, 26 November–15 December 1991, 26 January–8 February 1992, 9–31 October 1992, 24 November–10 December 1992, 11–27 January 1993). Tracking periods corresponded to three stages of the breeding season: when adults were incubating eggs in October (= 'incubation stage'); brooding chicks in November–December (= 'guard stage'); and rearing older chicks in January–February (= 'postguard stage'). Penguins at Long Point were radio-tracked during the latter stage of two seasons (1–15 February 1992, 2–12 February 1993).

Six penguins at Boulder Beach were fitted with radio-tags in February 1991. In 1991/92 and 1992/93, a further eight penguins were added to the sample of regularly radio-tracked birds, so that 14 individuals from eight breeding pairs were studied. Another penguin was radio-tagged once only, because its range was to the northeast of the eastern tracking station, so it could not be radio-tracked. Apart from February 1991, when one bird was apparently a nonbreeder, all study birds were breeding when first radio-tagged each year. If their breeding attempt subsequently failed, every effort was made to relocate the birds for further tagging and radio-tracking. Thirteen birds were radio tagged at Long Point in 1992 and 10 birds (including six from the previous season) in 1993. Three of the Long Point birds were failed breeders or non-breeders in 1992.

The radio transmitter packages (Sirtrack Electronics, Landcare Research, Havelock North, NZ) that were used measured 70 mm \times 35 mm \times 10 mm, weighed *c.* 42 g, and had a 280-mm long aerial. Each unit contained three 750 mA/h 3V lithium batteries in series which powered a 1mW transmitter for about six weeks. The units were glued to the lower back of penguins using a contact adhesive, Loctite 401, and removed two–three weeks later by peeling them away from the feathers.

To track bird movements at sea, two receiving stations were set up on either side of the breeding areas, approximately 15 km apart on the Otago Peninsula coastline, near Sandymount trig (319 m a.s.l.) and Cargills Castle (100 m), and on the Catlins coastline at Hinahina Cove (140 m a.s.l.) and Florence Hill (160 m). At each station a dual array of five-element Yagi antennae was mounted on a 3.25-m rotating mast, similar to that used by Hallberg *et al.* (1974). The antenna arrays were vertically polarised and wired 180° out of phase using 1/4 wavelength baluns. An adjustable protractor rose, marked in degrees, was clamped over a graticule in the base housing. Falcon V (Wildlife Materials, Carbodale, Illinois, USA) and TR-4 (Telonics Electronics Consultants, Mesa, Arizona, USA) biotelemetry receivers were used to monitor transmitter frequencies. Hourly radio-directions to each radio-tagged penguin were determined by locating the null between the two main peaks of signal amplitude simultaneously from each station. Signals were received only while birds were on the sea surface. Radio-tracking was generally done for periods of about seven hours a day (up to 16 hours for two days) during the tracking period. Bearings were relative to radio-directions of three land or island-based test transmitters from each station. Penguin positions at sea were later estimated by computer plotting the intersection of the radio bearings (program by R. Pickard, Department of Conservation, Wellington).

The accuracy of the radio-tracking system was tested in October 1992 by towing a dummy duck with a radio tag behind the Otago University research vessel *Munida* 6–40 km away from the tracking stations. The vessel made GPS satellite fixes of its position simultaneously with the radio-tracking team on land. There was a standard deviation of angular error of about 0.7° at each station. The mean distance between true location and that estimated from triangulation of radio bearings was 269 ± 155 m at 5–15 km ($n = 12$), 422 ± 228 m at 15–30 km ($n = 10$), and 1471 ± 455 m at 30–40 km ($n = 8$).

It was possible to track most birds when they were at sea using the two receiving stations, although one of the 14 penguins occasionally travelled out of tracking range to the northeast. Fixes were not accurate when radio-tagged penguins were

close to the coast, or when projections of the coast obscured the signals from one of the stations. This sometimes resulted in the program plotting locations on land. These points were deleted from the dataset. Occasional gross errors (caused by observers finding side nulls or back bearings) were also deleted.

Only the radio-tracking data of birds assumed to be foraging were used for subsequent analyses. Long dives ($>c.$ 100 s), which were usually associated with long surface times (*c.* 45 s), were assumed to be foraging dives. Not considered for analysis were locations of birds that were probably travelling (making short dive and surface times), diving for less than 100 s, giving constant signals while sitting on the surface and records where observers did not note the dive type.

The time that penguins spent at sea (foraging time) was estimated using data from an automatic data-logging station. This recorded the presence or absence of nine transmitter signals every 10 minutes at the study areas. The station had a fixed single array of five-element Yagi antenna on a 2.5-m mast. A box at the base of the mast contained a Control-03 data-logger (M. Wilson, Wellington Polytechnic, NZ), a Telomics TDP-2 data processor, a DOC-17 controller (M. Douglas, Department of Conservation, Wellington, NZ) and a battery. Foraging trip times were also obtained from time-depth recorders (three from Platypus Engineering, now Zelcon Technic, Glenorchy, Tasmania, Australia; two Mk5 recorders, Wildlife Computers, Redmond, WA, USA). These were deployed on three birds during the radio-tracking sessions of 1992/93 and four birds during equivalent periods of 1993/94 and 1994/95. Dive data *per se* are not dealt with in this paper.

The breeding success of study and non-study nests was monitored at Boulder Beach and Long Point. Nests were also monitored at areas with less human disturbance: at Sandfly Bay

($45^{\circ}54'S$, $170^{\circ}39'E$) on Otago Peninsula; Nugget Point ($46^{\circ}27'S$, $169^{\circ}49'E$) and Hayward Point ($46^{\circ}29'S$, $169^{\circ}43'E$) in the Catlins; Codfish Island ($46^{\circ}46'S$, $167^{\circ}38'E$) and Campbell Island ($52^{\circ}32'S$, $169^{\circ}10'E$).

An analysis of variance was calculated for the log of foraging time. The mean per bird for each stage in each year was used to compensate for the fact that some birds contributed more trips to the data than others. The ANOVA used the factors of year ($n = 5$), stage of breeding season ($n = 3$), sex ($n = 2$) and breeding success ($n = 3$: breeding and successful that year, breeding at the time of the trip but unsuccessful that year, and failed breeders or non-breeders), and two-factor interaction terms. A similar ANOVA was conducted on the mean maximum distance from the breeding area for each bird per day, using the same factors and interactions.

To test the effect of disturbance, a McNemar symmetry χ^2 was conducted on the breeding success data from 1991/92 to 1993/94 at Boulder Beach. This used a 3×3 table comparing chick production (0, 1 or 2 chicks fledged per nest) against disturbance type (transmitters/recorders plus diet samples, diet samples only or neither). Data from 1990/91 were not used as birds were not disturbed until late in the chick-rearing period; nor was data from 1994/95 used, because reliably successful birds were selected to carry dive recorders and this would have skewed the results.

RESULTS

Foraging time

Table 1 and Figure 2 summarise the foraging time data for all radio-tagged and dive recorded birds. It is evident that the majority (78%) of trips were less than 18 hours (median 14).

TABLE 1

Foraging time (hours) of breeding Yellow-eyed Penguins at Boulder Beach and Long Point

Year	Stage of breeding season	Foraging time (h)			No. of trips	No. of birds
		Median	Mean	s.d.		
Boulder Beach						
1990/91	postguard	14.4	16.4	9.0	43	5
1991/92	incubation	63.1	64.9	41.3	15	9
	guard	13.3	14.4	7.0	52	7
	postguard	14.4	15.9	5.4	28	5
1992/93	incubation	14.5	27.3	23.3	46	10
	guard	11.7	13.3	5.9	53	7
	postguard	14.0	14.4	6.8	92	9
1993/94	incubation	37.6	42.0	31.1	17	4
	guard	11.3	12.8	7.9	26	4
	postguard	13.2	16.0	8.5	21	3
1994/95	incubation	58.3	57.8	40.5	11	4
Long Point						
1991/92	postguard	14.0	13.5	5.4	41	5
1992/93	postguard	13.5	13.6	6.6	69	10
1993/94	postguard	6.7	8.1	4.8	35	3
Total		13.9	18.3	17.8	549	28

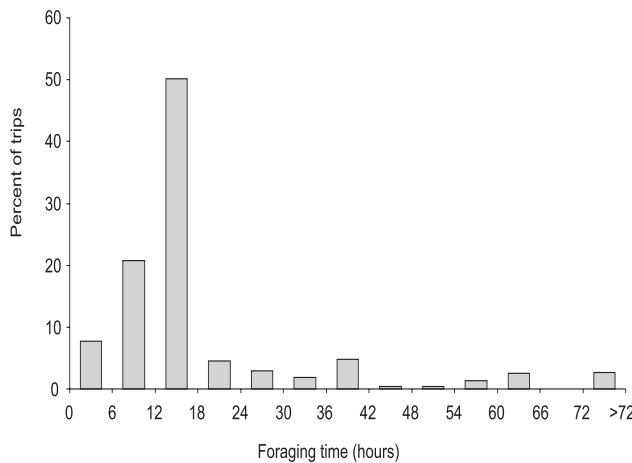


Fig. 2. Frequency distribution of foraging time of Yellow-eyed Penguins from Boulder Beach and Long Point, as determined by a presence-absence data-logger for radio-tagged birds or dive recorder information, 1990–1994 ($n = 549$ foraging trips). Bars are six-hour intervals except for >72 hours.

Pooling the data from all stages of the breeding season under-represents longer trips, since at the incubation stage it was usually only possible to record one or two foraging trips per bird.

Trips to sea at the incubation stage tended to be longer (median = 21.4, range 2.3–157.6 hours), and usually ranged from day-trips (leaving at dawn and returning at dusk) to staying out at sea for periods of two to three days. At this stage, breeding pairs alternated incubation duties at the nest. Trips during incubation in 1992/93 were shorter than those in other years (Table 1). There were some longer trips of 2–4 days duration in 1992/93 but most (61%) were less than 18 hours. In contrast, during the incubation periods of 1991/92, 1993/94 and 1994/95, 18, 47 and 23% of trips respectively were less than 18 hours long.

Trips at the guard stage tended to be relatively short (74% <18 hours; median 11.7, range 2–38 hours). At this time of the breeding cycle, when breeding birds were alternating chick-brooding duties at the nest, they had three main foraging patterns: at sea for the day (dawn till dusk), short trips in the evening, or out at sea overnight. Trips at the postguard stage, when chicks were left unattended and both partners of a pair were at sea simultaneously, were usually day-trips (median 13.8, range 1–56 hours).

An analysis of variance (see methods) was calculated for the log of foraging time at Boulder Beach to test whether it varied with the year, time of the year, sex or breeding status. In fact, all four factors were important as interaction terms, three of which had significant levels of variation: year*stage ($F_{4, 63} = 3.3, P < 0.05$), sex*breeding success ($F_{2, 63} = 3.4, P < 0.05$) and stage*breeding success ($F_{2, 63} = 3.7, P < 0.05$). Important influences on the variation were: short incubation shifts in 1992/93, as described above; failed breeders, especially the males, staying at sea longer than the other birds; breeders that would later fail taking longer trips during incubation than successful breeders; and failed breeders at the guard and postguard stages going to sea for longer than breeding birds. There were no significant differences overall between breeding males and females.

A similar analysis of variance for foraging time at the post-

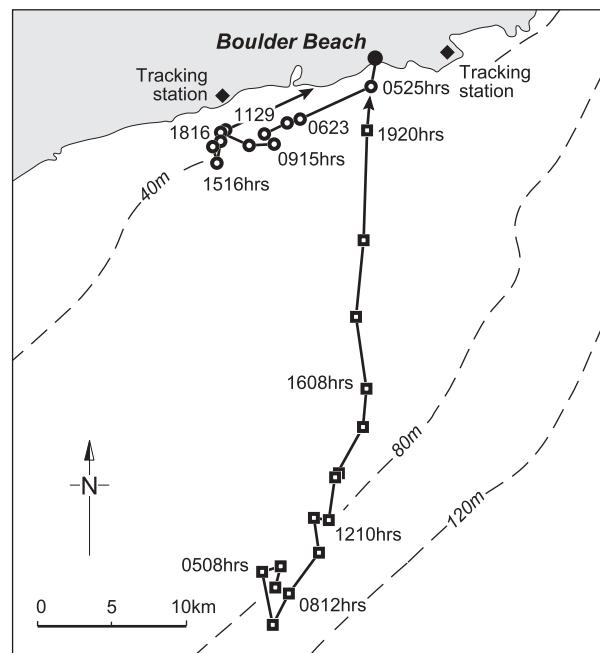


Fig. 3. Movements at sea of two radio-tagged Yellow-eyed Penguins from Boulder Beach, 22 October 1991. Each point is an hourly fix of the bird's position, as determined by intersection of simultaneous radio-bearings from the two tracking stations.

guard stage was calculated to test for differences between the two study areas. This found that birds at Boulder Beach were at sea for significantly longer ($F_{1, 34} = 6.3, P < 0.05$) than at Long Point. Few birds at Long Point went to sea for more than 18 hours (3% of trips), compared with 13% at Boulder Beach. Also, two individuals at Long Point usually went to sea twice (and sometimes three times) each day, particularly one bird in 1993/94, which resulted in significantly shorter average trip times that year ($F_{2, 34} = 5.0, P < 0.05$; Table 1).

Foraging range (Boulder Beach)

Figure 3 shows two examples of penguin movements at sea during a day's radio-tracking. The lines join the estimated points of intersection of radio-bearings at the hourly fixes for each bird. The offshore feeder was approximately 34 km from the breeding area at 05h08, when it had a constant signal on the surface (i.e. it had been resting at sea overnight). Most radio-fixes during the day were obtained when the bird was making long foraging dives, and moving up to 2 km between each hourly fix. After 16h08 it was travelling 5–7 km/h towards the breeding area. The other bird foraged closer to land, about 15 km along the coast from the breeding area. Usually, birds that left the breeding area at dawn moved quickly offshore but soon exhibited foraging behaviour (i.e. made long dives of 2–4 minutes duration) as they moved away from the coast.

Foraging zones during different stages of the 1991/92 and 1992/93 breeding seasons are illustrated by plots of the estimated foraging locations (Fig. 4). These show that the birds foraged south to southwest of the Boulder Beach breeding area, spreading out over the continental shelf, generally in water 40–80 m deep.

During incubation in 1991/92, when birds were making the

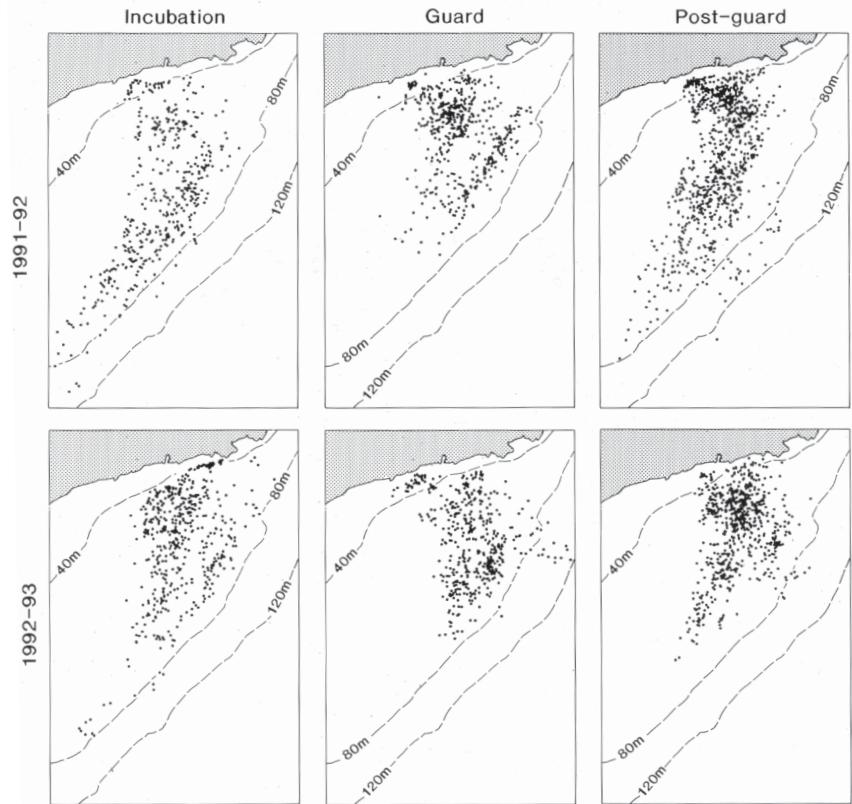


Fig. 4. Foraging locations (when birds were making long foraging-type dives) of all radio-tagged Yellow-eyed Penguins from Boulder Beach at three stages of the breeding season (incubation, guard and postguard) during two breeding seasons (1991/92, 1992/93).

longest trips to sea, their foraging locations were scattered widely, mostly 10–45 km (maximum of 57 km) from the breeding area (Fig. 4). This resulted in the highest median foraging distance for any tracking periods (Table 2). During the guard stage, most birds foraged closer to shore, with more movement to the southeast than during the earlier period. By the postguard stage, some birds concentrated their movements closer to the coast, but there was still a wide scatter of foraging locations.

In the 1992/93 breeding season there was some similarity with the previous year in the pattern of foraging at the different stages, but there was less long-distance foraging (Fig. 4). Only

9% of locations during incubation and 5% of locations during the postguard stage were >26 km from the breeding area, compared with 39% and 18%, respectively in 1991/92. For part of the incubation tracking period in 1992/93 it was noted that several birds foraged much closer to the coastline than usual.

The distance from the breeding area is an approximation of foraging range. Table 2 summarises the data for the distance of foraging locations away from the breeding area. The overall median foraging distance was 13.1 km at Boulder Beach and 11.0 km at Long Point. Because each bird's foraging location on a particular day was linked to the previous hourly fix, the data were reduced to the maximum distance reached

TABLE 2

Foraging distance (distance from breeding area when birds were undertaking long dives) and maximum distance per day of breeding radio-tagged Yellow-eyed Penguins at Boulder Beach and Long Point

Year	Stage of breeding season	Foraging distance (km)					Max. distance/day (km)				
		Median	Mean	s.d.	No. fixes	No. birds	Median	Mean	s.d.	No. fixes	No. birds
Boulder Beach											
1990/91	postguard	12.1	14.4	7.2	255	6	13.6	16.5	7.4	41	6
1991/92	incubation	22.2	23.3	11.2	455	13	25.1	26.3	11.3	86	13
	guard	12.1	13.4	6.1	334	10	14.6	15.4	6.9	73	10
	postguard	12.7	15.5	8.7	728	10	18.4	18.9	9.3	116	10
1992/93	incubation	12.4	14.0	8.6	522	14	15.0	16.9	9.8	91	14
	guard	14.9	14.4	5.8	315	10	15.6	15.6	6.3	80	10
	postguard	10.8	12.4	6.1	594	10	12.4	14.4	7.2	116	10
Long Point											
1991/92	postguard	12.0	11.1	7.2	321	9	13.8	13.3	8.1	70	9
1992/93	postguard	9.3	9.4	5.3	364	10	11.3	10.2	6.6	78	10

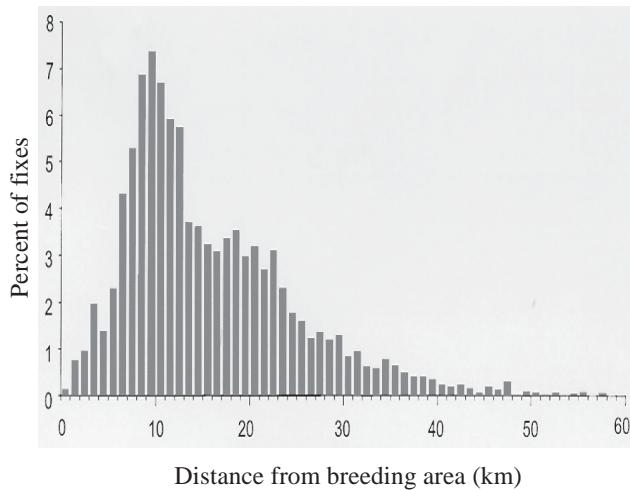


Fig. 5. Frequency distribution of distance at sea from the breeding area of all radio-tagged Yellow-eyed Penguins that were making foraging-type dives at the time of radio-tracking, 1990–1993 ($n = 3857$ locations).

per day. However, both data sets exhibit similar patterns, and support the trends described in Fig. 4. The overall median maximum distance per day was 15.7 km at Boulder Beach and 13.1 km at Long Point. Figure 5 shows a frequency distribution of distance for foraging locations during all years and stages of the breeding season at Boulder Beach. Note that a high proportion (50%) of locations were less than 13 km from the breeding area, a further 38% were 13–26 km away, and 12% were more than 26 km away.

An analysis of variance (see methods) was calculated for the

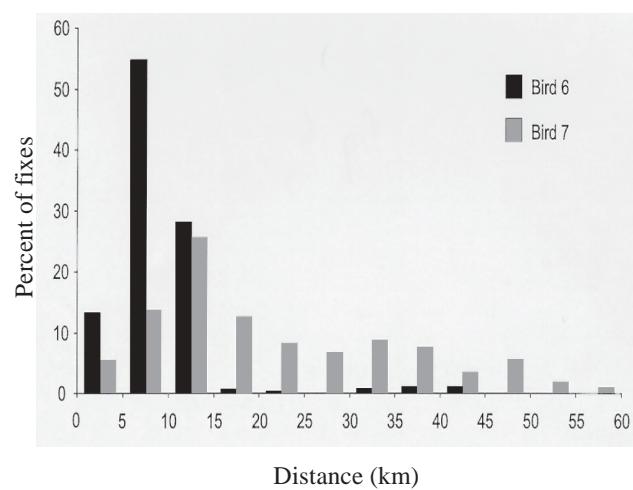


Fig. 6. Frequency distribution of distance at sea (5-km intervals) from the breeding area of two radio-tagged Yellow-eyed Penguins (birds 6, 7). Data pooled from seven radio-tracking periods in three years, 1990–1993.

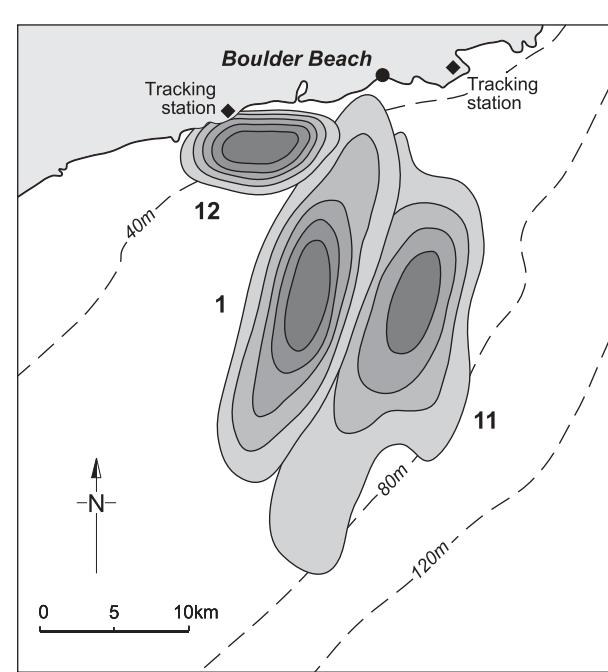


Fig. 7. Foraging ranges of three individual Yellow-eyed Penguins (birds 1, 11, 12) as estimated by Epanechnikov density kernels (Silverman 1986). The central contour estimates the most frequently used part of the foraging range. Data pooled from foraging location radio-fixes over seven radio-tracking periods in three years, 1990–1993.

mean maximum distance from the breeding area for each bird per day at Boulder Beach. This was to test whether foraging distance varied with the year, time of the year, sex or breeding status. All four factors were involved in the two interaction terms which showed significant variation: year*stage ($F_{2,76} = 6.1, P < 0.01$) and sex*breeding success ($F_{2,76} = 6.6, P < 0.01$). Variation in the first interaction was mainly caused by birds travelling farther at the incubation (and to a lesser extent the postguard) stage of 1991/92 than in 1992/93. In contrast, birds during the incubation stage of 1992/93 travelled similar distances to those at later stages of the year. The second interaction was a result of successful breeding females foraging closer to shore than other females (failed breeders or breeders that would later fail), yet there was no corresponding pattern for males.

The median foraging distance at the postguard stage for both years at Long Point was 13.1 km, which is similar to Boulder Beach at the same stage (13.9 km). Analysis of variance of mean maximum distance per bird found no significant difference between the two areas.

Individual foraging range at Boulder Beach

Each radio-tagged penguin showed individual differences in foraging range and direction travelled each day, which they generally retained at different times of the year and between years. The frequency distributions of locations from all tracking periods of two birds are shown in Figure 6. One penguin (bird 6) tended to forage less than 15 km from the breeding area, whereas the other (bird 7) tended to forage more widely. Three examples of individual ranges which have little overlap are shown in Figure 7. These are contour diagrams of density estimates of the foraging location points, using Epanechnikov kernels (Silverman 1986, Worton 1989). The central contour provides an estimate for the most frequently used part of the foraging range. If the central contours of the foraging location data are used, there is overlap of birds in the midshelf area, as birds tended to move along the SSW axis from Boulder Beach (Fig. 8). However, there is separation into groupings, with two strongly inshore-oriented birds (<5 km from the nearest coastline), eight with midshelf tendencies (5–16 km) and four with more outer shelf tendencies (>16 km from the nearest coast-

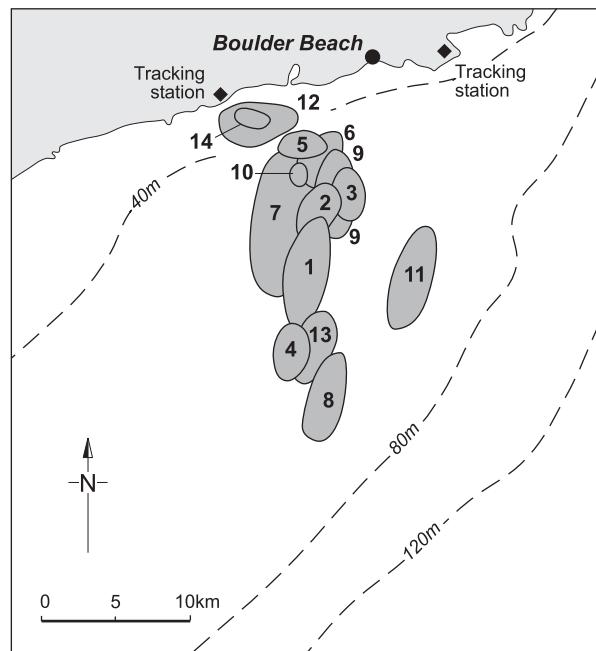


Fig. 8. Foraging range centres of activity (central contours of density kernels) of 14 radio-tagged Yellow-eyed Penguins during seven radio-tracking periods in three years, 1990–1993.

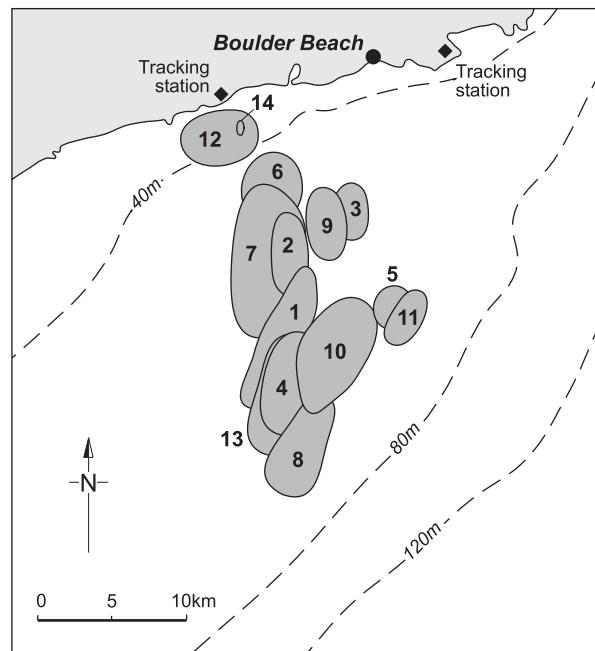


Fig. 9. Maximum distance per day density kernel centres of 14 radio-tagged Yellow-eyed Penguins during seven radio-tracking periods in three years, 1990–1993.

line). If maximum distance per day is plotted, there is further spread of the central contours towards the outer shelf (Fig. 9); i.e. some birds that spent most of their time in the midshelf area (e.g., birds 5, 10, 13; Fig. 8) frequently travelled to the outer shelf during their foraging trips (Fig. 9).

Individual foraging range at Long Point

Foraging ranges at Long Point during the postguard stage of the breeding season showed some similarities to Boulder Beach in that foraging locations were spread out over the flatter part of the continental shelf, but this tended to be in deeper water (80–120 m; Fig. 10) than at Boulder Beach (Figs. 7–9). The central contours of the Epanechnikov kernel density estimators show three birds with strong inshore tendencies, nine midshelf and threeoutershell feeders (Fig. 10). Six of the 14 birds were radio-tracked in both years, and four of these retained the same type of foraging pattern from year to year. The other two switched from being outer shelf to midshelf feeders.

Breeding success

Breeding success is summarised in Table 3 (see also Moore & Wakelin 1997). Nest failures were a result of infertility or disappearance of eggs, and starvation, trampling, or predation (probably by introduced Stoats *Mustela erminea*, Ferrets *M. furo* or Domestic Cats *Felis catus*) of chicks, but often the cause of failure was uncertain. A comparison is also provided for monitored nests on Codfish Island (southern New Zealand) and the sub-Antarctic Campbell Island (Table 3). Breeding success in 1992/93 was relatively high at all sites.

Disturbance and possible impacts on breeding success

At Boulder Beach, disturbed nests (adults carrying packages and captured for diet samples or adults that were captured for

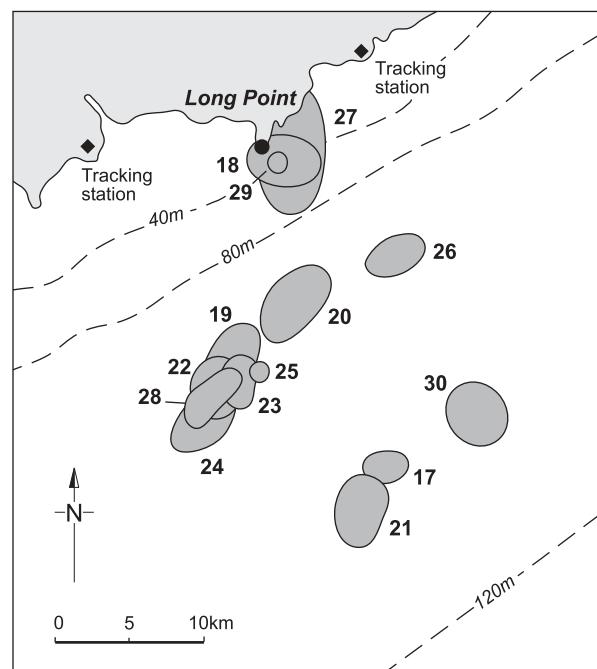


Fig. 10. Foraging range centres of activity (central contours of density kernels) of 14 radio-tagged Yellow-eyed Penguins during two radio-tracking periods, at the post-guard stage of 1991/92 and 1992/93.

diet samples only) had lower levels of breeding success than other nests (Table 3; $\chi^2 = 8.2$, d.f. 3, $P = 0.042$ – see methods). Although nests with transmitters had the highest level of disturbance (birds handled up to eight times per breeding season, packages taken on and off, several diet samples taken), they had higher average success than nests with adults that

were disturbed only once or twice each year for diet collection (Table 3). Six out of the eight pairs of birds with transmitters produced one or two chicks each year (mean number of chicks fledged per nest = 1.1, n = 24 nesting attempts for the eight pairs) but their success did not improve in years when they were not disturbed (mean chicks = 1.0, n = 10). In contrast, nesting attempts that were disturbed by diet sampling had a mean chick production of 0.6 chicks per nest, yet the same pairs had a mean success of 1.52 chicks per nest (n = 25 nesting attempts) in following years.

There was apparently little effect on breeding success by the application of transmitters to Long Point birds (Table 3) late in the chick period. Nests with adults that were captured for diet samples had higher success in 1992/93 than 1991/92. It was less common at Long Point than Boulder Beach for the same individuals to be disturbed in this manner more than once per year or in consecutive years.

DISCUSSION

Prior to this study, it was considered that Yellow-eyed Penguins fed away from the coast (van Heezik 1990) between 7–13 km offshore (Seddon & van Heezik 1990). Smith (1987) related Yellow-eyed Penguin distributions to the wide areas of continental shelves (>14 km wide) and high levels of primary

production. At Boulder Beach and Long Point, the shelf is about 35 km wide. This may be a productive zone for penguin prey, as a wide area of medium-sized pebbles in the midshelf region (Andrews 1973) has a distinctive and species-rich benthic fauna (Probert & Batham 1979, Probert & Wilson 1984). Also, the cool subtropical Southland Current flows northeast along the coast, influencing the zooplankton and fish spawning that occurs there (Jillett 1969, 1976, Robertson 1980).

Foraging range estimation from radio-telemetry has confirmed the importance of the continental shelf. Dive depth data has also shown the importance of foraging at or near the bottom (Moore *et al.* 1995, P.J. Moore unpubl. data) and analysis of the diet composition shows the importance of bottom-dwelling prey such as Opalfish *Hemerocoetes monopterygius* (Moore & Wakelin 1997).

Tracking of penguins indicated that most had habitual foraging patterns. Whether this reflects the favouring of particular areas or some other factors, such as the birds taking a similar heading to sea each day, is not known. However, the inshore feeders, in particular, showed a very fixed habit of not moving far from the coastline. These birds at Boulder Beach ate proportionally more Blue Cod *Parapercis colias* and Sprat *Sprattus antipodum* and less Opalfish and Arrow Squid than did the midshelf and outer shelf birds (Moore & Wakelin

TABLE 3

Yellow-eyed Penguin nesting success at different levels of disturbance and localities

Locality	1990/91 ^a		1991/92		1992/93		1993/94		1994/95		All years	
	No. chicks	No. nests ^c /nest ^b	No. chicks	No. nests	No. chicks	No. nests	No. chicks	No. nests	No. chicks	No. nests	No. chicks	No. nests
	/nest ^b		/nest		/nest		/nest		/nest		/nest	
Boulder Beach												
tx nests ^d	1.0	3	0.75	8	1.25	8	0.8	5	2.0	3	1.07	27
diet nests ^e	1.0	1	0.67	3	0.43	7	0.64	11	—	—	0.59	22
other nests ^f	0.64	11	1.4	15	1.5	12	1.47	15	1.44	27	1.34	80
Sandfly Bay	0.57	7	1.27	15	1.67	15	0.85	13	1.13	16	1.17	66
Otago Total	0.68	22	1.17	41	1.33	42	1.0	44	1.37	46	1.16	195
Long Point												
tx nests ^d	—	—	1.5	4	1.8	5	1.33	3	—	—	1.58	12
diet nests ^e	—	—	0.67	6	1.56	9	—	—	—	—	1.2	15
other nests ^f	0.36	11	0.92	12	1.29	17	1.34	32	1.42	38	1.22	110
Nugget/Hayward Point ^f	0.27	11	0.75	16	1.4	15	1.58	12	1.44	16	1.11	70
Catlins Total	0.32	22	0.87	38	1.43	46	1.4	47	1.43	54	1.2	207
Codfish Island ^f	—	—	0.5	10	1.17	18	0.9	21	1.18	20	1.0	69
Campbell Island ^f	—	—	0.58	36	1.5	26	—	—	—	—	0.97	62

^a Most nests were reduced to single eggs by Dept. of Conservation staff, so chick production was low that year.

^b Mean number of chicks fledged per nest.

^c Number of nests found during the egg stage and monitored for breeding success.

^d Nests where one or both adults had transmitters or dive recorders attached during study periods. (multiple handling of birds and diet samples at Boulder Beach).

^e Nests where one or both adults had diet sample(s) taken during the year.

^f Nests which were monitored only.

1997). There were some similarities in the diet of inshore feeders between birds from Boulder Beach and Long Point, but at the latter area they ate more Arrow Squid *Nototodarous sloani* than their offshore counterparts. The midshelf birds ate the most Opalfish, and the outershelf birds ate the most Silverside *Argentina elongata* (Moore & Wakelin 1997).

The 1992/93 season provided an example of the possible effects of diet and availability of food on breeding success. There were significant differences in penguin diet composition compared with other years for several prey species, such as an increase in Red Cod *Pseudophycis batus*, and decreases in Blue Cod and Arrow Squid (Moore & Wakelin 1997). A similar dietary shift by Yellow-eyed Penguins in the mid-1980s was suggested as being a response to the availability of higher quality food (van Heezik 1990). The pattern of foraging range and times in 1992/93 also differed from other years, with trips tending to be shorter and closer to shore. These changes – better quality food and easier foraging – may have contributed to the high breeding success in that year.

Foraging behaviour and ranges of penguins vary with the biology of the species, environmental conditions and the nature of the food supply. The Yellow-eyed Penguin was said to occupy the 'inshore' niche that the Gentoo Penguin *Pygoscelis papua* occupies elsewhere (Croxall & Lishman 1987). This is probably an oversimplification as the Gentoo does not exclusively hold this niche (Williams 1995) and it is a shallow to deep water diver which feeds mainly on pelagic krill (Trivelpiece *et al.* 1987, Williams 1995), whereas the Yellow-eyed Penguin feeds mainly on bottom-dwelling fish of the continental shelf. The two species do, however, share characteristics such as nonmigratory behaviour, short nest reliefs, nonfasting, and slow growth of chicks, which are probably adaptations to the relatively mild climatic conditions prevailing at the centre of their ranges (Trivelpiece *et al.* 1987).

Within its latitudinal range, the Yellow-eyed Penguin is absent from areas with little continental shelf (Smith 1987). It is 'replaced' by the Fiordland Crested *Eudyptes pachyrhynchus* and Snares Crested *E. robustus* Penguins, which apparently forage inshore for pelagic prey during the breeding season (Cooper *et al.* 1990, van Heezik 1989, Williams 1995).

The penguin body is highly streamlined (Bannasch 1995) and several studies have highlighted the effects of package attachment on swimming and diving efficiency (e.g. Wilson *et al.* 1986, Croll *et al.* 1991). Small, streamlined devices attached to penguins can increase the energy required for swimming by 25% (Culik & Wilson 1991). To some extent penguins may be able to compensate for the increased amount of drag, since the effects on foraging trip duration can be negligible (Gales *et al.* 1990, Croll *et al.* 1996, Hull 1997) but still may increase the rate of nest desertion (Croll *et al.* 1996). Not surprisingly, large devices without any streamlining result in longer trips and nest failures (Croll *et al.* 1996, Hull 1997). The disturbance caused by collecting diet samples has received less attention, but the removal of one meal from adults had no effect on foraging duration or breeding success of Adélie Penguins *Pygoscelis adeliae* (Robertson *et al.* 1994).

Carrying packages may also have affected Yellow-eyed Penguin foraging behaviour during this study. Birds that travelled for longer and further than average tended to fail in their breeding attempt, and this was possibly influenced by their decreased swimming efficiency. There was a more certain effect on breeding success, since birds with packages and/or

diet samples produced fewer chicks than birds from undisturbed nests. However, the highly disturbed group of birds had better breeding success than those that were only occasionally captured to collect diet samples. This suggests that there was habituation to disturbance or that the individuals that were diet sampled were prone to disturbance because more of them were new breeders (the area was recovering subsequent to a population crash).

One could predict that in a year of difficult foraging, the effects of disturbance would be compounded. Furthermore, birds will forage for longer and farther afield in a poor year, which will influence their breeding success. Because adults will work harder for less or lower quality food, their chicks may starve, and they will be less able to cope with other environmental pressures (e.g. toxins, disease, heat stress or predators). For example, since no definitive cause was found at the time of the die-off of Yellow-eyed Penguins in 1990 (Gill & Darby 1993), there may have been a compounding of factors. A warm period possibly affected the food chain and penguin diet (Moore & Wakelin 1997) and/or influenced an avian malaria outbreak (Graczyk *et al.* 1995).

ACKNOWLEDGEMENTS

Thanks are due to Bruce McKinlay, Dean Nelson, Mike Wakelin, Murray Douglas, Brian Murphy for their sterling efforts with the radio-tracking. Thanks also for the occasional help provided by Vernon Trainor and Peter Dann (Otago 1991/92), Geoff Aimers (Otago 1992/93), Wendy Hamilton (Catlins 1991/92) and Davina Hunt (Catlins 1992/93). The various landowners of Otago Peninsula and Catlins kindly allowed access to penguin areas or to sites for our receiving stations. Ross Pickard gave help and advice with computing, and David Fletcher with statistics. Helpful comments on drafts were made by Ralph Powlesland, Chris Pugsley, Don Newman, Lloyd Davis and an anonymous referee.

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