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Predation by New Zealand sea lions (*Phocarctos hookeri*) as a threat to the viability of yellow-eyed penguins (*Megadyptes antipodes*) at Otago Peninsula, New Zealand

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ABSTRACT

This study presented evidence that creates a quandary for conservation management: predation by one threatened species, New Zealand sea lion (*Phocarctos hookeri*), threatens the viability of another threatened species, yellow-eyed penguin (*Megadyptes antipodes*), at Otago Peninsula, South Island, New Zealand. Otago Peninsula holds the largest population of yellow-eyed penguins on South Island and the only breeding population of New Zealand sea lions on the New Zealand mainland. New Zealand sea lions here represent the vanguard of re-colonisation within their prehistoric range, with nine females and 50–70 males resident in 2005. The initial indication of a potential problem was an attack on a yellow-eyed penguin by a New Zealand sea lion witnessed in 1996. The majority of 20 records for attacks were at two neighbouring sites, where they coincided with decreases in penguin nest numbers and adult annual survival. In contrast, penguin nest numbers increased at a third site, the main base for male sea lions at Otago Peninsula. Evidence from prey remains indicated that male sea lions did not eat yellow-eyed penguins but that females ate 20–30 annually, with one individual possibly responsible for most kills. Modelling indicated that the penguin population at any one site could not remain viable if it was the sole source of penguins killed. The dilemma is either to do nothing, and risk collapse of the Otago Peninsula population of yellow-eyed penguins, or to take action against known culprits, and risk failure in re-colonisation of the New Zealand mainland by New Zealand sea lions.

1. Introduction

Yellow-eyed penguins (*Megadyptes antipodes*) and New Zealand sea lions (*Phocarctos hookeri*, also known as Hooker's sea lions) have breeding distributions restricted to the southern New Zealand region, from the eastern coast of South Island (Fig. 1) south to Campbell Island (52°S, 169°E) (Marchant and Higgins, 1990; Wilkinson et al., 2003). Both species are designated as 'threatened' under IUCN criteria. Yellow-eyed penguins are designated as 'endangered', primarily because they are subject to extreme fluctuations in numbers and their total area of occupancy is small (Stattersfield and Capper, 2000). Otago Peninsula (Fig. 1) holds the largest population of yellow-eyed penguins on South Island (McClung et al.,

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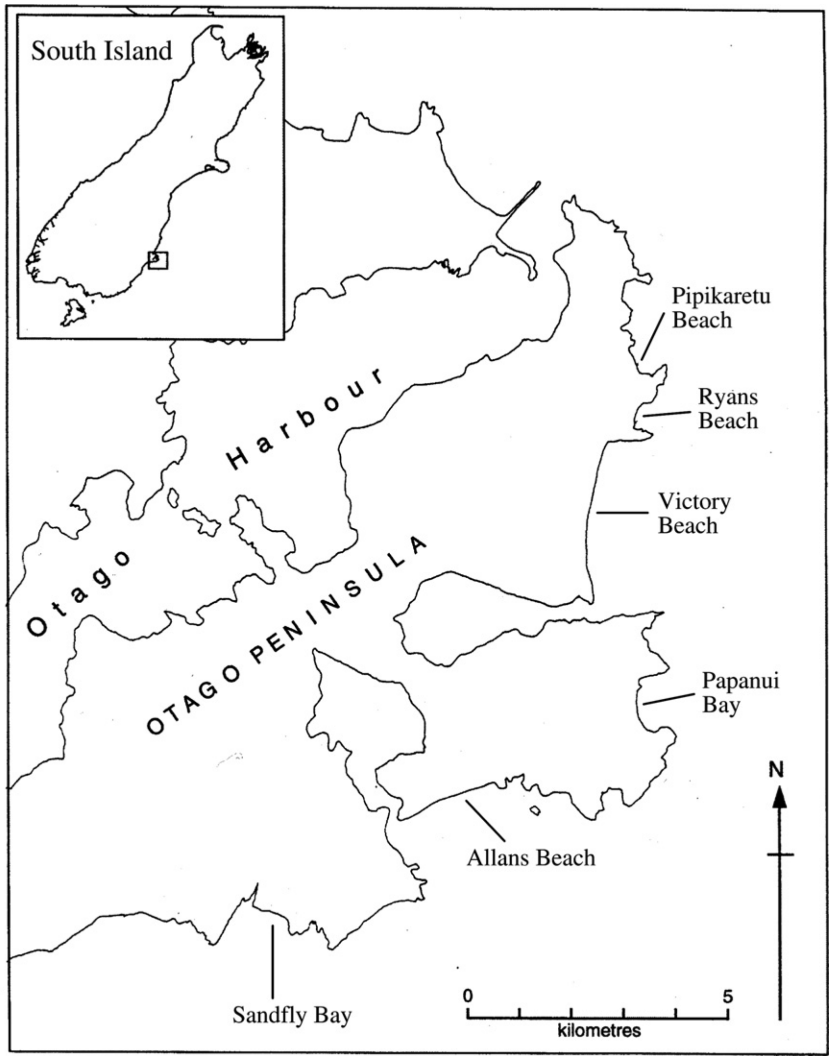

Fig. 1 – Map of Otago Peninsula, South Island, New Zealand, showing the locations of beaches mentioned in the text.

2004), with about 200 nests annually (Marchant and Higgins, 1990). New Zealand sea lions are designated as 'vulnerable' because breeding is restricted to less than 5 locations (Lalas and Bradshaw, 2003; Wilkinson et al., 2003). Otago Peninsula marks the northern limit of a continuous presence of New Zealand sea lions that began in about 1980, representing a re-colonisation of South Island following extirpation of the species by humans about 150 years ago, and breeding began there in 1993/94 (McConkey et al., 2002a,b; Lalas and Bradshaw, 2003). The ongoing increase in numbers of New Zealand sea lions at South Island is attributable to the combination of immigration from the south, almost exclusively by males (McConkey et al., 2002a), and to pup production at or near Otago Peninsula, the origin for practically all resident females (McConkey et al., 2002b; Lalas and Bradshaw, 2003).

Attacks on yellow-eyed penguins by New Zealand sea lions have been witnessed and described from the northern and southern ends of their distributions, at Otago Peninsula (Schweigman and Darby, 1997) and at Campbell Island where this predation was considered a probable cause for a decrease in recorded numbers of yellow-eyed penguins (Moore, 1992; Moore and Moffat, 1992). Predation by New Zealand sea lions was not among the list of threats to yellow-eyed penguins in Stattersfield and Capper (2000) and in the New Zealand Department of Conservation policy statement on the management of this species (McKinlay, 2001). Yellow-eyed penguins were not listed as prey in the only quantitative assessment of the diet of New Zealand sea lions at Auckland Islands (51°S, 166°E), the species population base, but unidentified bird remains were found in 2% of 142 scats and 64 regurgitations analysed (Childerhouse et al., 2003). Although otariid seals (Pinnipedia: Otariidae, fur seals and sea lions) have been widely reported as predators of penguins, only one quantitative example has shown that this impact can be substantial: predation by Cape fur seals (*Arctocephalus pusillus*) threatens the survival of small populations of African penguins (*Spheniscus demersus*) in South Africa (Marks et al., 1997; Crawford et al., 2001; David et al., 2003). A precedent for a substantial impact of predation by New Zealand sea lions on a prey species was reported from Macquarie Island (54°S, 159°E), the western tip of their distribution, where one subadult male killed up to 43% of fur seal pup production (*Arctocephalus* 2 spp.) in one year (Robinson et al., 1999).

We investigated the possibility that predation by New Zealand sea lions is a threat to the viability of yellow-eyed penguins at Otago Peninsula. This study was prompted by recent unprecedented declines in penguin nest numbers at two adjacent sites, Pipikaretu Beach (45° 48′S, 170° 45′E) and Ryans Beach (45° 49′S, 170° 45′E), Otago Peninsula (Fig. 1). Monitoring at these two study sites began in 1984, with continual annual increases in yellow-eyed penguin nest numbers through to 1996 (Ratz and Thompson, 1999; Ratz et al., 2004). Fatal attacks on yellow-eyed penguins by New Zealand sea lions witnessed near these two colonies raised the possibility that predation by sea lions may have been responsible for the decline in penguin numbers. For comparison, we assessed trends at a third study site, Papanui Beach (45° 52′S, 170° 44′E; Fig. 1), the main base for male New Zealand sea lions at Otago Peninsula (McConkey et al., 2002a), where continual monitoring of yellow-eyed penguins began in 1995 (McKay et al., 1999).

The possibility that a threatened species jeopardises the viability of another threatened species presents a nightmare for conservation management. Commercial implications further complicate this conundrum. Two of our three study sites are destinations for ecotourism ventures: about 50,000 tourists visit Pipikaretu Beach annually with *Penguin Place* tours (landowner H. McGrouther pers. comm. to HR) and about 15,000 tourists visit Papanui Beach annually with *Elm Tours* (landowner D. McKay pers. comm. to CL). Collapses in the numbers of yellow-eyed penguins at these sites could jeopardise the viability of these ventures. We registered that we were unlikely to produce definitive results or emphatic recommendations. Instead, we modified a population model for yellow-eyed penguins by Efford and Edge (1998) to create simulations for the maximum sustainable predation rate by New Zealand sea lions.

2. Methods

2.1. Management of yellow-eyed penguins at the three study sites

Habitat, dispersion of nests and conservation management of yellow-eyed penguins were described for Pipikaretu Beach and Ryans Beach by Ratz and Thompson (1999) and for Papanui Beach by McKay et al. (1999). The three study sites are in close proximity with Pipikaretu Beach and Ryans Beach less than 1 km apart, with Papanui Beach 5 km further south (Fig. 1). Proximity alone does not generate valid comparisons among sites. Here we highlight similarities and differences among our sites by addressing the main threats to yellow-eyed penguins and the causes of population fluctuations, as itemised in Stattersfield and Capper (2000) and described more extensively in McKinlay (2001).

(a) Degradation of breeding habitat by land clearance
Management of breeding habitat is similar at all three study sites but differs from the recommended techniques of fencing to exclude farm stock followed by restoration of native vegetation. Instead, breeding habitat is in pasture and shrubland grazed by sheep (*Ovis aries*) and supplemented with the provision of artificial nests sites. Habitat restoration is restricted to native vegetation planted around nest sites.

(b) Predation of penguin chicks by introduced mammals
Trapping and shooting has mitigated the threat of predation of chicks and no substantial predation events occurred at any of the three sites during the study period, with a no more than four chicks killed annually.

(c) Drowning of penguins in monofilament gill-nets at sea
Penguins at sea off Otago Peninsula forage over the continental shelf, typically 5–16 km from the coast (Moore, 1999). Penguins departing to sea or returning to shore risk drowning in recreational nets set close to shore off breeding sites and foraging penguins risk drowning in commercial nets set further offshore (Darby and Dawson, 2000). To our knowledge, no nets have been set close to shore off any of our study sites. Deployment of nets set further offshore remains unknown. Given that typical distances travelled to foraging zones exceed the separation of the study sites, we suggest that these nets are likely to affect all three sites similarly.

(d) Human disturbance of penguins ashore
Unregulated public access has had a detrimental affect on yellow-eyed penguins in the Department of Conservation reserve at Sandfly Bay (45° 50′S, 170° 36′E; Fig. 1), Otago Peninsula (McClung et al., 2004). All our three study sites are on private land where landowners prohibit unsupervised public access. Two of our sites are destinations for ecotourism ventures: *Penguin Place* at Pipikaretu Beach since 1992 and *Elm Tours* at Papanui Beach since 1998. Ratz and Thompson (1999) used our other study site, Ryans Beach, as a control site and showed that the tours at neighbouring Pipikaretu Beach did not have a detrimental effect on yellow-eyed penguins.

(e) Population crashes due to food shortages
The most recent population crash at Otago Peninsula attributed to food shortages was in 1986 and 1987 (Marchant and Higgins, 1990). The close proximity of our three study sites minimises any likelihood of differences in food availability. These three sites share the similarity that they are the only sites at Otago Peninsula where emaciated penguins are treated and rehabilitated, at Pipikaretu Beach and Ryans Beach (Ratz and Thompson, 1999) by landowner H. McGrouther since 1988 (pers. comm. to HR) and at Papanui Beach by landowner D. McKay since 1999 (CL pers. obs.).

(f) Population crashes due to disease
The most recent population crash at Otago Peninsula due to disease was in 1990 and attributed to avian malaria (Graczyk et al., 1995).

2.2. Monitoring of yellow-eyed penguins

We refer to two age classes of yellow-eyed penguins, “juveniles” and “adults”. Juveniles, penguins in their first year after fledging, are distinguished from adults, penguins more than 1 year old, by differences in head plumage (Marchant and Higgins, 1990). Nest numbers at Pipikaretu Beach and at Ryans Beach, recorded from the 1984/85 to the 1996/97 breeding seasons by Ratz and Thompson (1999) and Ratz et al. (2004), were updated to 2004/05. Monitoring of marked individuals to deduce annual survival of breeders at these two locations began in the 1992/93 breeding season with comprehensive banding of birds with numbered, stainless steel flipper bands as described in Ratz et al. (2004). Annual survival of breeders was designated as the survival from the beginning of one breeding season to the beginning of the next for adults that nested at least once, updating data in Ratz et al. (2004) to 2003/04, the survival through 12 months from the start of the 2003/04 breeding season. No breeders moved to other sites but up to 6% of breeders skipped breeding in any one season (Ratz et al., 2004; Ratz, unpublished data). Nests at Papanui Beach were monitored annually from 1995/96 to 2004/05, following McKay et al. (1999), but no annual survival data were available because the penguin population was unmarked. Monitoring at Papanui Beach included nests on neighbouring private land abutting the northwestern end of the zone depicted in McKay et al. (1999).

Temporal trends in nest numbers were estimated with exponential curves in the form $y \propto e^{\lambda x}$, where λ = average exponential annual growth rate. Annual growth rates were presented as average arithmetic rates (μ), where $\mu = e^{\lambda} - 1$, following Gerrodette (1987). Calculations of 95% confidence intervals (the likely spread of the line of best fit) and 95% prediction intervals (the likely spread of data) for trends followed Mendenhall (1988). We treated data for annual survival of breeders as binomial distributions, with calculations for 95% confidence intervals following Zar (1999).

2.3. Monitoring of New Zealand sea lions

Male and female New Zealand sea lions were analysed separately to deduce trends in their distribution and abundance at Otago Peninsula. We calculated trends for males from annual maxima in monthly counts of number seen ashore at Otago Peninsula and the number seen ashore in the same monthly count at their main base, Papanui Beach. These data formed a discontinuous series collated from various sources: Hawke (1986) for 1984–1985, Beentjes (1989) for 1986–1987, Lalas (1997) for 1991–1992, McConkey (in litt.) for 1994, McConkey (1997) for 1995 and McConkey (unpublished data) for 1996–1999 and 2002–2004. All females were individually identifiable and seen continually throughout the study. Results were presented as absolute numbers of known individuals, updating McConkey et al. (2002b) and Lalas and Bradshaw (2003).

Prey of New Zealand sea lions at Otago Peninsula were identified and analysed from diagnostic, indigestible remains found in scats and regurgitations, following techniques in Lalas (1997). Ongoing systematic monthly sampling of the diet of male New Zealand sea lions deduced from collections of scats and regurgitations began at Papanui Beach in May 1991. In addition to the first year of sampling (Lalas, 1997), we have completed analyses of these monthly samples only for the most recent year, 288 scats and 73 regurgitations from June 2004 to May 2005. These analyses included only prey items with an estimated original mass greater than 20 g. This nominal mass was designated because no prey items were found in the range 20–50 g. Smaller items could have been of secondary origin, in the stomach contents of larger prey, and their inclusion would have skewed estimates for average prey mass.

Opportunistic collections of prey remains elsewhere at Otago Peninsula began in 1992 with typically 2–4 collections annually at Victory Beach (45° 51′S, 170° 43′E; Fig. 1), coinciding with the initiation of continual use of this site by New Zealand sea lions. Victory Beach subsequently became the main base for females at Otago Peninsula (McConkey et al., 2002b). Here females ashore frequented a radiata pine (*Pinus radiata*) forestry plantation abutting dunes at the south end of the beach, a zone rarely used by males older than pups. This separation of the sexes ashore facilitated a systematic study of the diet of female New Zealand sea lions at Victory Beach, initiated in July 2003. The aim through the first month was familiarisation with the dispersion of females ashore, typically spread through about 6 ha, and the removal of all old prey remains. All scats and regurgitations then were collected for 10 consecutive days per month for five months, August–December 2003. Scats and regurgitations from the first day of monthly sampling included remains that had accumulated since the previous collection. Regurgitations collected later during the consecutive days of searching were less than 1 day old and therefore designated as “fresh”. Fresh regurgitations found beside (less than 2 m) a female were allocated to that female.

We divided remains of yellow-eyed penguins as prey of New Zealand sea lions into two categories: unconsumed remains and regurgitated (consumed) remains. We collected and collated records for witnessed fatal attacks on yellow-eyed penguins by New Zealand sea lions and categorised any subsequent unconsumed remains found washed ashore. From these remains we concluded that finding fresh yellow-eyed penguin pelt (skin with feathers attached), head or limbs washed ashore were indicative of a recent kill by a New Zealand sea lion.

2.4. Population models

Efford and Edge (1998) presented a population model for yellow-eyed penguins at Otago Peninsula with a scenario that simulated an annual growth rate of 6% ($\mu = 0.060$), regarded as a realistic intrinsic growth rate for this species. This is the only published population model for the species and its realism remains untested. We ran simulations of this model in Leslie matrix model spreadsheets in *Microsoft Excel*. We increased values for annual mortality of juveniles and adults to produce an annual population growth rate of zero, and so generated estimates for the annual kill rate that resulted in long-term stability in penguin nest numbers instead of a 6% annual increase.

Lalas and Bradshaw (2003) presented a model for growth of the female population of New Zealand sea lions at Otago Peninsula derived from data up to 2002. We updated these data to 2006 and ran simulations using the likely maximum annual increase of 13% ($\mu = 1.127$) and the likely minimum annual increase of 7% ($\mu = 1.067$), respectively scenarios M18 and M19 from Table 3 in Lalas and Bradshaw (2003). We simulated the effects of removal of adult females by progressively deleting all five locally-born females alive and at least four years old in 2006.

3. Results

3.1. *Trends in yellow-eyed penguin nest numbers at three locations*

The three monitored yellow-eyed penguin breeding locations at Otago Peninsula showed statistically significant temporal trends in annual nest numbers (Fig. 2). Pipikaretu Beach and Ryans Beach exhibited average annual increases in nest numbers from 1984/85 to 1996/97 of 10% ($n = 13$, $r = 0.926$, $p < 0.001$, $\lambda = 0.096$) and 12% ($n = 10$, $r = 0.837$, $p < 0.01$, $\lambda = 0.109$), respectively. Pipikaretu Beach then exhibited an average annual decrease in nest numbers from 1996/97 to 2004/05 of 10% ($n = 9$, $r = 0.872$, $p < 0.01$, $\lambda = -0.106$). Ryans Beach exhibited an average annual decrease in nest numbers from 1996/97 to 2002/03 of 7% ($n = 7$, $r = 0.813$, $p < 0.01$, $\lambda = -0.076$). Numbers at Ryans Beach for the last two seasons, 2003/04 and 2004/05, were excluded from the statistical analysis and fell below the −95% confidence limit of earlier years (Fig. 2).

Numbers at Pipikaretu Beach dropped to 15 nests in 2004/05, 41% of their peak of 37 nests in 1996/97 (Fig. 2). Decreases at Ryans Beach were more dramatic, dropping to 12 nests in 2003/04 and to three nests in 2004/05, respectively 35% and 9% of their peak 34 nests in 1996/97 and 1997/98 (Fig. 2). In contrast to Pipikaretu Beach and Ryans Beach, Papanui Beach exhibited an average annual increase in nest numbers from 1995/96 to 2004/05 of 3% ($n = 10$, $r = 0.783$, $p < 0.01$, $\lambda = 0.033$), without any indication of a decrease through the later years (Fig. 2).

Excluding the last two breeding seasons (2003/04 and 2004/05), we deduced a statistically significant linear relationship in annual yellow-eyed penguin nest numbers between Ryans Beach and Pipikaretu Beach ($n = 16$, $r = 0.885$, $p < 0.001$, $y = 0.84x$), indicating that nest numbers at these two locations followed similar trends (Fig. 3). When the last two breeding seasons were superimposed on this graph, the result for 2004/05 fell below the lower 95% confidence limit delineated by the relationship (Fig. 3). Trends in yellow-eyed penguin annual survival of breeders appeared similar at Pipikaretu Beach and Ryans Beach, with the exception of drastic reductions at Ryans Beach for 2002/03 and 2003/04 (Table 1, Fig. 4). Lower survival rates at Ryans Beach in these last two years were statistically significant ($Z_c = 3.194$, $p < 0.01$ for 2002/03; $Z_c = 2.490$,

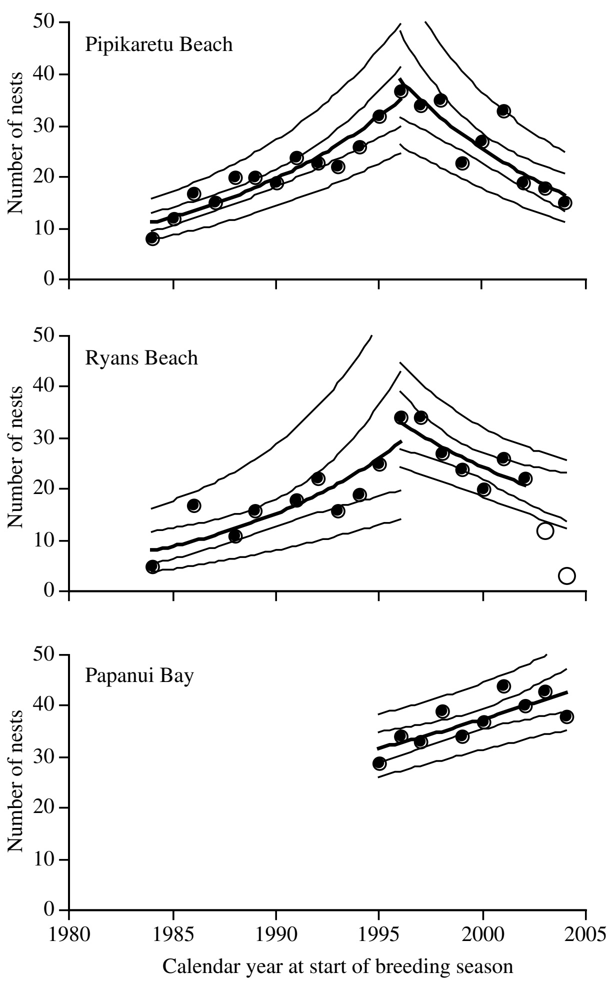

Fig. 2 – Trends in yellow-eyed penguin nest numbers at three locations: exponential growth curves of best fit, where $y \propto e^{\lambda x}$. Inner pairs of lines delineate 95% confidence intervals and outer pairs of lines delineate 95% prediction intervals. Numbers at Ryans Beach for 2003 and 2004 (white circles) were excluded from analyses.

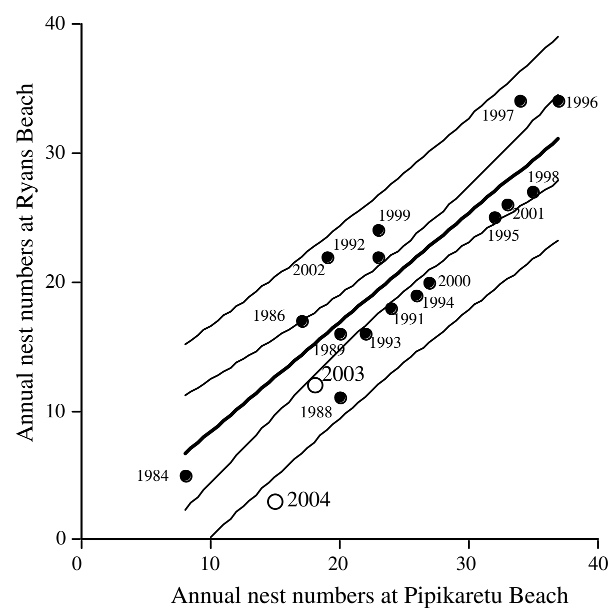

Fig. 3 – Linear relationship between Ryans Beach and Pipikaretu Beach for the number of yellow-eyed penguin nests for the 16 breeding seasons with data for both beaches, 1984/85 to 2002/03. The inner pair of lines delineates the 95% confidence interval and the outer pair of lines delineates the 95% prediction interval. The year adjacent a data point indicates calendar year at start of breeding season. Two additional data points, 2003 and 2004 (white circles), were not included in analyses.

Table 1 – Data for annual survival of yellow-eyed penguin breeders at Pipikaretu Beach and Ryans Beach through 12 consecutive years, September 1992 to September 2004

Year start (September)	Pipikaretu number at start	Pipikaretu number at end	Ryans number at start	Ryans number at end
1992	42	37	31	30
1993	44	39	31	24
1994	44	41	38	28
1995	59	55	46	36
1996	73	55	67	51
1997	64	57	62	46
1998	64	49	45	31
1999	46	42	40	35
2000	52	48	39	31
2001	66	45	50	38
2002	38	33	43	22
2003	36	25	24	8

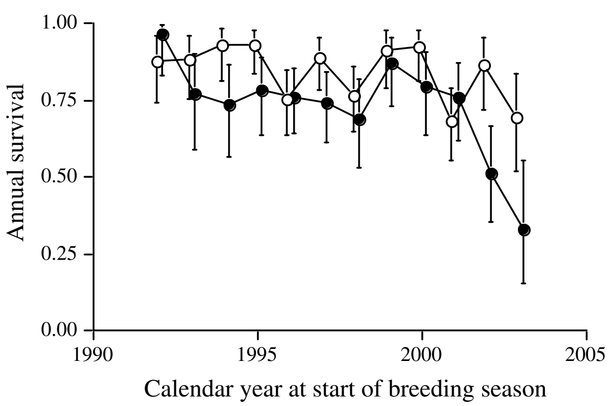

Fig. 4 – Annual survival of yellow-eyed penguin breeders at Pipikaretu Beach (white circles) and Ryans Beach (black circles) through 12 consecutive years from the start of the 1992/93 breeding season (1992) to the start of the 2004/05 breeding season (2003).

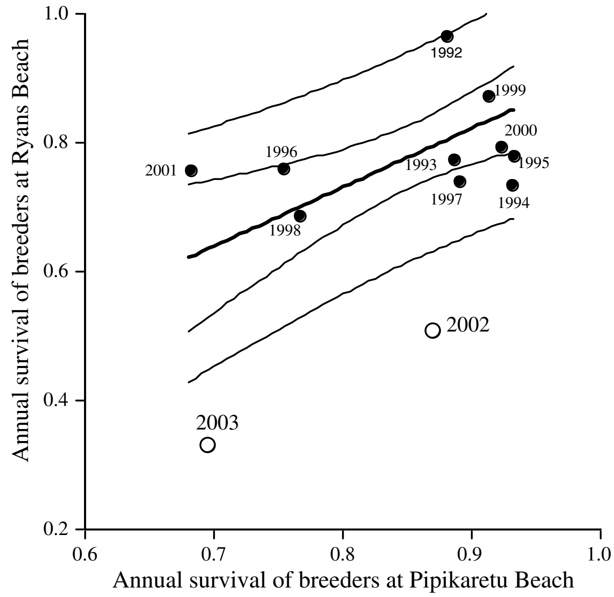

Fig. 5 – Linear relationship between Ryans Beach and Pipikaretu Beach for annual survival of yellow-eyed penguin breeders for 10 consecutive years from the start of the 1992/93 breeding season (1992) to the start of the 2002/03 breeding season (2001). The inner pair of lines delineates the 95% confidence interval and the outer pair of lines delineates the 95% prediction interval. The year adjacent a data point indicates calendar year at start of breeding season. Two additional data points, 2002 and 2003 (white circles), were not included in analyses.

$p < 0.05$ for 2003/04; sample sizes in Table 1). Excluding 2002/03 and 2003/04, we found a statistically significant linear relationship in unweighted means for annual survival of breeders between Ryans Beach and Pipikaretu Beach ($n = 10$, $r = 0.637$, $p < 0.05$, $y = 0.91x$), reinforcing that annual survival of breeders at these two locations followed similar trends (Fig. 5). When the data for the last two years breeding seasons were superimposed on this graph, both fell below the lower 95% confidence limit delineated by the relationship. Annual adult survival of breeders at Ryans Beach averaged 91% that at Pipikaretu Beach through earlier years. However, this proportion dropped to 59% for 2002/03 and to 48% for 2003/04 (Fig. 5).

3.2. *Trends in numbers of New Zealand sea lions at Otago Peninsula*

Annual maxima for counts of male New Zealand sea lions seen ashore at Otago Peninsula increased from about 5 in the mid-1980s to about 40 in recent years, at an average annual increase of 11% from 1984 to 2004 ($n = 15$, $r = 0.958$, $p < 0.001$, $\lambda = 0.107$) (Fig. 6). The respective annual increase at Papanui Beach was 10% ($n = 15$, $r = 0.959$, $p < 0.001$, $\lambda = 0.091$) (Fig. 6). All males were based at Papanui Beach until the early 1990s when additional locations, primarily Victory Beach and Sandfly Bay (Fig. 1), were occupied as numbers increased. Ratios deduced from exponential curves in Fig. 6 for the period 2001–2004 indicated that an average 70–75% of males at Otago Peninsula were based at Papanui Beach.

Updating data for breeding presented in Lalas and Bradshaw (2003) to include 2005/06, a total of 28–29 pups have been born at or near Otago Peninsula. All were born to the founding female, her eldest three daughters and her eldest three granddaughters. Pups were raised at Otago Peninsula, typically at Victory Beach. In June 2006 this female population (excluding pups) totalled six adults at least four years old and five younger individuals at 1–3 years old.

3.3. *Attacks on yellow-eyed penguins by New Zealand sea lions at Otago Peninsula*

To our knowledge, all attacks on yellow-eyed penguins witnessed from shore were attributable to New Zealand sea lions. We collated evidence for 20 fatal attacks on yellow-eyed penguins by New Zealand sea lions at Otago Peninsula up to October 2005 (Table 2), beginning with the two records by Schweigman and Darby (1997). Site totals north to south were Pipikaretu Beach (7), Ryans Beach (6), Victory Beach (1), Papa-

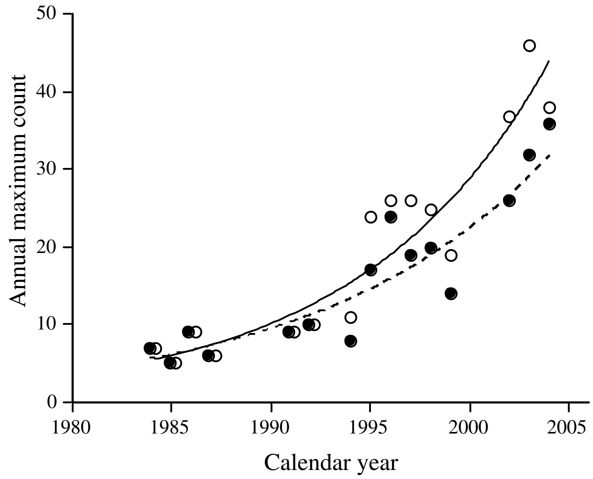

Fig. 6 – Annual maxima for counts of male New Zealand sea lions seen ashore at Papanui Beach (black circles) and at all sites on Otago Peninsula (white circles) through 15 years from 1984 to 2004.

nui Beach (5) and Sandfly Bay (1). There was a higher likelihood for a sea lion kill to be witnessed, and remains recovered ashore, at Pipikaretu Beach or Papanui Beach than at Ryans Beach because the former two sites were viewed daily by guided tour groups while Ryans Beach was monitored regularly only from September to April, with 1–2 visits weekly.

All seven witnessed attacks were in the surf zone off sandy beaches that abutted breeding areas. Unconsumed remains of penguins were found washed ashore following four of these witnessed attacks and on 13 other occasions. Ten of the 17 unconsumed remains consisted only of pieces of pelt (skin with feathers attached) that varied in size from 5×2 cm to 30×20 cm. One penguin was found as an articulated skeleton with the pelt inverted over the head, a category carcass designated as "degloving" by Marks et al. (1997). Five of the other six remains included the head and two included a leg. Five adults and two juveniles were aged, either during a witnessed attack and/or from retrieved heads.

3.4. *Prey of male New Zealand sea lions at Otago Peninsula*

No remains of yellow-eyed penguins were found through the 14 years of systematic monthly sampling of scats and regurgitations from male New Zealand sea lions at Papanui Beach from June 1991 to May 2005 (CL unpublished data). Similarly, no yellow-eyed penguins were represented among any prey remains collected opportunistically from male sea lions elsewhere on Otago Peninsula (CL unpublished data). Analyses of monthly samples from Papanui Beach for the most recent year, June 2004 to May 2005 produced a total of approximately 651 invertebrates and fish greater than 20 g, with an estimated total original mass of approximately 490 kg: 258 swimming crabs (*Ovalipes catharus*), total mass 27 kg, average 0.1 kg, largest 0.3 kg; 137 cephalopods, total mass 223 kg, average 1.6 kg, largest a 12 kg octopus (*Pinnoctopus cordiformis*); and 256 fish, total mass 240 kg, average 0.9 kg, largest a 7 kg rough skate (*Raja nasuta*). (Salps, especially *Pyrosoma atlanticum*, accounted for approximately 382 (97%) of the approximately 393 prey items less than 20 g.) These samples also contained remains of two seabirds and approximately 12 New Zealand fur seals. The seabirds were represented by feathers from

Table 2 – List of witnessed fatal attacks on yellow-eyed penguins by New Zealand sea lions, and of unconsumed penguin remains found washed ashore, at Otago Peninsula

Date	Location	Penguin age (if known)	Attack witnessed?	Remains collected ashore
18 Nov 1996[a]	Sandfly Bay		Yes	None
28 May 1997[a]	Papanui Beach	Juvenile	Yes	None
15 May 1998[b]	Papanui Beach	Adult	Yes	Degloved body
12 Jan 2000	Ryans Beach		No	Pelt
15 May 2000	Pipikaretu Beach	Adult	Yes	Pelt and head
4 Feb 2001	Pipikaretu Beach		Yes	None
30 Sep 2001[b]	Papanui Beach	Adult	Yes	Pelt and head
7 Jan 2002	Ryans Beach		No	Pelt
17 Jan 2002	Pipikaretu Beach	Adult	No	Pelt, head, 1 leg
18 Feb 2002	Ryans Beach		No	Pelt
22 Mar 2002	Pipikaretu Beach		No	Pelt
10 Feb 2003	Ryans Beach		No	Pelt
8 Mar 2004	Pipikaretu Beach		No	Pelt
13 Apr 2004	Pipikaretu Beach		No	Pelt
24 Apr 2004	Ryans Beach		No	Pelt
22 Feb 2005	Victory Beach		No	Pelt
28 Apr 2005	Pipikaretu Beach	Adult	Yes	Pelt and head
17 May 2005	Papanui Beach		No	1 leg
13 Jun 2005	Ryans Beach		No	Pelt
2 Oct 2005	Papanui Beach	Juvenile	No	Pelt and head

a From Schweigman and Darby (1997).
b B. Templeton (pers. comm. to CL).

one blue penguin (*Eudyptula minor*) and one spotted shag (*Stictocarbo punctatus*). The New Zealand fur seals were represented by scraps of pelt and bones that included remains of animals older than pups. Quantified evidence for predation on large New Zealand fur seals came from Pipikaretu Beach, where *Penguin Place* staff (pers. comm. to HR) witnessed three attacks on New Zealand fur seals in the surf zone at weekly intervals during November 2003. Their degloved bodies washed ashore and measured (by CL and HR) as males 123, 138 and 152 cm standard length (linear measure from nose to tail).

3.5. Yellow-eyed penguins as prey of female New Zealand sea lions at Otago Peninsula

Regurgitated remains of yellow-eyed penguins were found in prey remains collected opportunistically from female New Zealand sea lions at Victory Beach. These remains consisted of a mass of loose feathers regurgitated to form a flat circle or oval typically 20–40 cm across, or a cylinder typically 10–20 cm long, and/or regurgitated patches of pelt up to 25 × 15 cm. Our first record was on 1 February 2001 and consisted of freshly regurgitated (moist) feathers beside two adult females, the two eldest offspring of the founder female, and their pups lying together in the pine plantation at the south end of the beach. Since then, regurgitated yellow-eyed penguin remains were found continually at this site, with the most recent in June 2005, but only one regurgitation collected opportunistically was attributable to a particular sea lion: SDMcC saw the eldest daughter of the founder female regurgitate yellow-eyed penguin feathers on 15 September 2004.

Female New Zealand sea lions ate at least 10 yellow-eyed penguins during the 5-month systematic study at Victory Beach, August–December 2003 (Table 3). Excluding pups, seven different females were encountered, including four adults (at least four years old). Three of five fresh regurgitations containing yellow-eyed penguin feathers and/or pelt were beside the eldest daughter of the founder female, an adult with a pup, and none were near other sea lions. The only other birds represented in prey remains were from three spotted shags, with their feathers found in regurgitations in August, September and November. Our only definitive record for another sea lion having eaten a yellow-eyed penguin was for the eldest daughter of the founder female's second daughter. We found regurgitated feathers near this female, aged three years, at Allans Beach (Fig. 1) on 10 October 2005.

3.6. Sustainable rates of predation by New Zealand sea lions on yellow-eyed penguins

Theoretically, small yellow-eyed penguin populations corresponding to 1–50 nests annually could sustain annual losses of up to 18% of their juveniles and adults without a long-term decrease in nest numbers (Fig. 7). Erring on the side of caution, the lower 95% prediction limit of annual losses of up to 11% annually could be regarded more realistic for these small populations (Fig. 7). Extrapolating beyond 50 nests annually (x), larger populations theoretically could sustain annual losses (y) of up to 20% of their juveniles and adults annually ($y = 0.196x$).

Extrapolations from Table 3 indicated that female New Zealand sea lions at Otago Peninsula killed 20–30 yellow-eyed penguins annually. Simulations of the impact of this annual kill rate of yellow-eyed penguins by New Zealand sea lions predicted the collapse of penguin populations with fewer than 100 nests annually (Fig. 8). Populations averaging 25 nests annually, for example Ryans Beach or Pipikaretu Beach, theoretically could sustain 4–5 kills annually, but collapsed to extinction in five years at a rate of 20 kills annually. A penguin population with 100 nests annually could theoretically sustain 19–20 kills annually, but not 25 kills. A yellow-eyed pen-

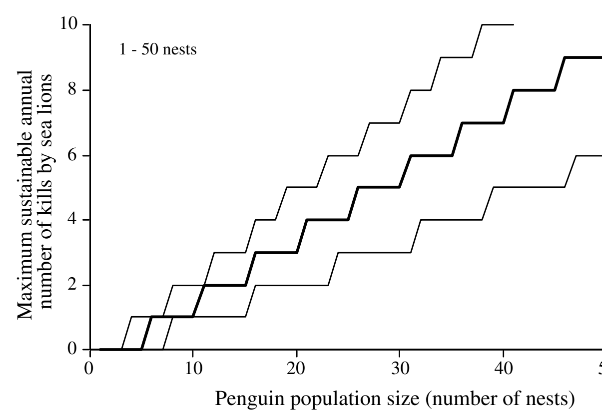

Fig. 7 – Prediction for the maximum number of kills by New Zealand sea lions (y) sustainable by yellow-eyed penguin populations corresponding to ⩽50 nests annually (x). The estimate, y = 0.182x, is flanked by ±95% prediction intervals, y = 0.251x, and y = 0.114x, respectively.

Table 3 – Minimum number of yellow-eyed penguin represented in regurgitations from female New Zealand sea lions at Victory Beach through five consecutive months, August–December 2003

Month (2003)	Month total	From fresh regurgitations	Fresh regurgitations beside a sea lion?
August	4	2	2 beside 0350
September	2	1	No
October	0	–	–
November	2	1	1 beside 0350
December	2	1	No
Total (5 months)	10	5	3 beside 0350

Fresh regurgitations were <1 day old. "0350" = eldest daughter of the founder female at Otago.

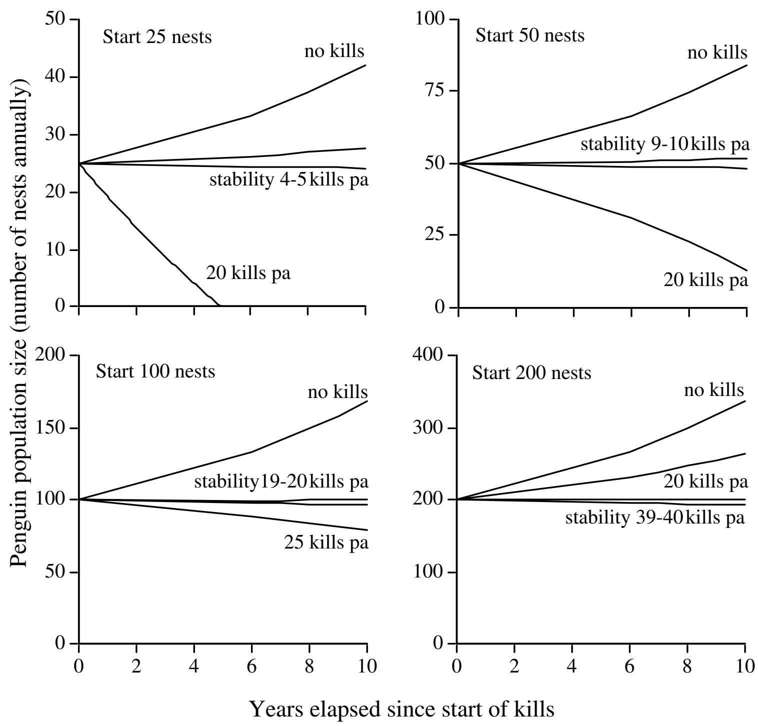

Fig. 8 – Simulations of the effects of the annual kill of yellow-eyed penguins by New Zealand sea lions on four penguin populations through 10 years following the start of kills.

guin population size corresponding to 200 nests annually, an approximation for the Otago Peninsula population, theoretically could sustain up to 40 kills annually (Fig. 8).

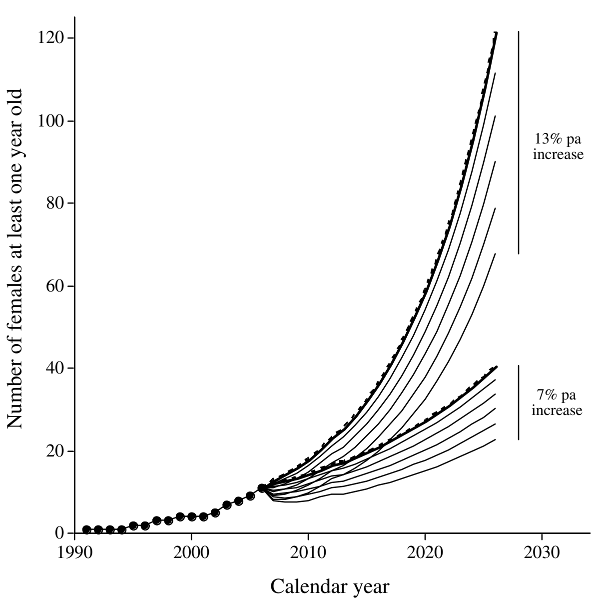

Fig. 9 – Recorded increase in the number of female New Zealand sea lions based at Otago Peninsula (black circles) extrapolated 20 years from 2006 for maximum (13%) and minimum (7%) likely annual rates of increase. Dashed line represent respective increases without removal of any females, each followed by five solid lines representing removal of 1–5 adult females in 2006.

3.7. *Effects of removal of female New Zealand sea lions on their population growth*

One option to reduce the rate of predation by New Zealand sea lions on yellow-eyed penguins at Otago Peninsula is to remove the female identified as responsible for most of the kills. The present annual rate of increase of this female population visually matched the Otago likely maximum scenario of 13% in Lalas and Bradshaw (2003) (Fig. 9). Theoretically, removal of 1–5 of the locally-born adult females in 2006 would not weaken their long-term population viability. These scenarios assume that removal of individuals would not alter the patterns of dispersal, survival and recruitment of younger females. Although removal of any one female is unlikely to alter the behaviour of the remainder, we cannot hypothesise on the impact of multiple removals.

4. Discussion

We documented long-term trends in nest numbers of yellow-eyed penguins at three study sites with similar habitats and conservation management at Otago Peninsula, South Island, New Zealand. All three sites were on private land that prohibited unsupervised public access. Pipikaretu Beach and Papanui Beach were sites for visits by ecotourism ventures; with Ryans Beach monitored as a control site to test for any effects of tourism at neighbouring Pipikaretu Beach (Ratz and Thompson, 1999). Nest numbers of yellow-eyed penguins at Pipikaretu Beach and Ryans Beach increased steadily from 1984/85 to 1996/97 but then decreased through subsequent years. The recent collapse in nest numbers at

Ryans Beach followed a drastic reduction in annual survival of breeders. In contrast, nest numbers at Papanui Beach increased steadily through the recent years of decrease at the other two sites.

The male population of New Zealand sea lions at Otago Peninsula has increased at about 10% annually since 1984, with about 70–75% based at Papanui Beach through recent years. We have yet to analyse data to determine absolute abundance but expect that 50–70 male New Zealand sea lions at least one year old were based at Otago Peninsula in 2005 (SDMcC and CL, unpublished data). The female population of New Zealand sea lions at Otago Peninsula has increased at about 13% annually since breeding began in 1993/94. Continuing the pattern described in McConkey et al. (2002b), all six female New Zealand sea lions that raised pups at Otago Peninsula were based primarily at the south end of Victory Beach, midway between Ryans Beach and Papanui Beach and within 3 km of each of our three yellow-eyed penguin study sites.

We derived an estimate for rate of predation from the occurrence of consumed remains of yellow-eyed penguins in scats and regurgitations from New Zealand sea lions, rather than using records for unconsumed remains. Marks et al. (1997) used the systematic daily collection of unconsumed remains of seabirds that washed ashore after kills by seals as an estimate for a minimum rate of predation. We could not use this method because we did not systematically inspect beaches daily. However, there was a higher likelihood for a kill to be witnessed, and remains recovered ashore, at Pipikaretu Beach (7 kills recorded) and Papanui Beach (5 kills) than at Ryans Beach (6 kills) because the former two sites were viewed daily by guided tour groups, while Ryans Beach was monitored regularly only from September to April, with 1–2 visits weekly.

No remains of yellow-eyed penguins were found in prey remains from male New Zealand sea lions at Papanui Beach and elsewhere at Otago Peninsula. The size of yellow-eyed penguins did not preclude them as prey. Their typical mass of 5–6 kg (Marchant and Higgins, 1990), is half that of the largest invertebrates and fish recorded as prey of New Zealand sea lions, respectively a 12 kg octopus (this study) and an 11 kg ling (*Genypterus blacodes*) (Lalas, 1997). The irrelevance of size becomes even more apparent in comparison with fur seals as prey. Records of 10+ kg fur seal pups as prey at Macquarie Island (Robinson et al., 1999) and Otago Peninsula (Bradshaw et al., 1998) were superseded by our records in this study for larger New Zealand fur seals up to 152 cm standard length, corresponding to a mass of approximately 80 kg (estimated from Fig. 2 in Dickie and Dawson, 2003).

The simplest explanation for the absence of yellow-eyed penguins among prey remains of male New Zealand sea lions at Otago Peninsula is that the male rarely ate any seabirds, with only two recorded in our analysis of their diet. Previous reports of witnessed attacks on yellow-eyed penguins by New Zealand sea lions attributed kills to males (Moore and Moffat, 1992; Schweigman and Darby, 1997). In contrast, we did not find any evidence to indicate that males impacted detrimentally on nest numbers of yellow-eyed penguins. Instead, penguin nest numbers increased at Papanui Beach, the main base for an increasing population of male New Zealand sea lions at Otago Peninsula, through recent years when penguin nest numbers decreased at Pipikaretu Beach and Ryans Beach. However, our results do not preclude the possibility that males might target yellow-eyed penguins.

Evidence of yellow-eyed penguins in opportunistic collections of prey remains attributable to female New Zealand sea lions were found continually at Victory Beach beginning in February 2001. A systematic study of prey remains from female New Zealand sea lions at Victory Beach indicated that females ate 10 yellow-eyed penguins in five months, equivalent to 20–30 annually. All records of penguin remains attributed to a particular sea lion at Victory Beach involved the same individual and included the first record in 2001. This raised the possibility that one sea lion, a female, was responsible for most of the predation. This female was the eldest daughter of the founder female and the first pup recorded born on South Island following extirpation of the species by humans about 150 years ago (McConkey et al., 2002b; Lalas and Bradshaw, 2003). This female has been, and continues to be, a key individual in the re-colonisation of South Island by New Zealand sea lions. She has produced six pups from 1997/98 to 2005/06, including four females all recorded alive in June 2006, and her eldest daughter had her first pup in 2004/05 (SMcC and CL, unpublished data). Our only other verification of another sea lion at Otago Peninsula having eaten a yellow-eyed penguin came in October 2005 and was for a locally-born three year old female. This one record not only implicated the next generation but also showed that young females are capable of eating the penguins.

The hypothetical allocation of all yellow-eyed penguins eaten to one adult female sea lion can give an insight into their relevance as prey. Applying a mean body mass of 114 kg for adult female New Zealand sea lions (Gales and Mattlin, 1997) to Eq. (19) in Innes et al. (1987) for daily consumption rate of adult otariid seals produced an estimate for annual consumption of 2.3 t. The estimate of 20–30 penguins at 5–6 kg equated to 100–180 kg annually, corresponding to only 4–8% of the annual consumption of one adult female New Zealand sea lion. This shows that a rate of predation that threatens the viability of a penguin population forms only a small contribution to the food requirement for one sea lion.

Simulations of the impact of this annual kill rate predicted the extirpation of penguin populations corresponding to fewer than 100 nests annually before the start of predation. Yellow-eyed penguins breed at 14 sites at Otago Peninsula (Marchant and Higgins, 1990), the largest with 74 nests recorded in the mid-1980s (Moore, 2001). Consequently, no site could remain viable if it were the sole target for predation of yellow-eyed penguins by New Zealand sea lions. However, an Otago Peninsula yellow-eyed penguin population with about 200 nests annually (McClung et al., 2004) theoretically could sustain up to 40 kills annually. Although it may sustain the present annual kill of 20–30 penguins by one individual, this population could not remain viable if two or more New Zealand sea lions targeted yellow-eyed penguins as prey.

Otago Peninsula holds the largest population of yellow-eyed penguins on South Island, approximately 10% of the species total population of 1780–2090 breeding pairs (McKinlay, 2001), and the only breeding population of New Zealand sea lions on the New Zealand mainland. Here the likelihood that one threatened species, New Zealand sea lion, threatens the viability of another threatened species, yellow-eyed penguin, presents a quandary for conservation management. This quandary is further complicated by two facts: the only sea lions known to have eaten yellow-eyed penguins are two females, and a collapse in penguin numbers at Pipikaretu Beach would destroy the *Penguin Place* ecotourism venture that caters for 50,000 tourists annually. The dilemma is obvious: either do nothing, and risk collapse of the Otago Peninsula population of yellow-eyed penguins, or take action against the individual sea lion(s) known to eat the penguins, and risk failure in the re-colonisation of the New Zealand mainland by New Zealand sea lions.

In 1997 New Zealand sea lions were designated as threatened species under provisions in the Marine Mammals Protection Act 1978, a status that requires human-induced threats to be minimised in order to promote an increase in numbers and colonisation of new breeding locations (Wilkinson et al., 2003). Otago Peninsula is of relevance as the only place likely to be designated as a "new breeding location" for New Zealand sea lions in the foreseeable future (Lalas and Bradshaw, 2003). The same Act also allows for a legalised kill of marine mammals under permit, an action that has a precedent with two New Zealand fur seals legally shot in 1998 (Lalas and Bradshaw, 2001). Culling individuals witnessed killing seabirds has reduced the impact of seal predation on seabirds in South Africa (David et al., 2003). A legalised kill of New Zealand sea lions could be a feasible solution if the individuals perceived as problem animals were males but is unacceptable for females, the vanguard for a new breeding location. An alternative to killing problem animals is translocation, the transfer of native animals to new locations within their natural distribution (Linnell et al., 1997). However, these translocations generally fail (Fischer and Lindenmayer, 2000). In particular, translocated otariid seals typically return to their capture site (Ridgway and Robinson, 1985; Gentry, 1998; Fraker and Mate, 1999). Consequently, translocation seems unlikely as a viable option.

A continuation of this study is unlikely to produce results in the short term that are more definitive than those already presented. We recommend an immediate decision for action and present two options. First, do nothing. This is an acceptable response given that the two species were sympatric in Otago before extirpation of sea lions by humans. Under this paradigm, the present threat to viability of yellow-eyed penguins is an unfortunate but natural event. Second, eliminate the immediate problem by transferring the female responsible into captivity. We have shown that the removal of this female is unlikely to jeopardise the viability breeding by New Zealand sea lions at Otago Peninsula. This should be the preferred response under the paradigm that anthropogenic impacts on yellow-eyed penguins have crippled the ability of the species to sustain further losses.

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