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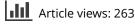
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Movements by stoats (*Mustela erminea*) and ferrets (*M. furo*) through rank grass of yellow-eyed penguin (*Megadyptes antipodes*) breeding areas

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Abstract Predation by introduced stoats (Mustela erminea) and ferrets (M. furo) may be contributing to the decline of yellow-eyed penguins (Megadyptes antipodes) on the South Island of New Zealand. Areas of rank grass were established in the hope of reducing predation by physically excluding predators from penguin breeding areas. This paper describes a foot-print tracking study which showed that stoats and ferrets were recorded twice and ten times respectively more often in rank grass than in grazed pasture. Stoats moved evenly throughout the rank grass, but ferrets restricted their movements to tracks through the rank grass. Ferrets approached penguin nests over 12 times more often than randomly selected sites in grazed pasture, particularly in spring when the penguin chicks are vulnerable to predation. Stoats appeared to avoid areas with high ferret abundance. Mice (Mus musculus), an important prey of these predators, were recorded 5-17 times more often in the ungrazed areas than in grazed areas. The concentration of stoats, ferrets and mice in the penguin breeding areas surrounded by rank grass increases the number of encounters between penguin chicks and predators, and so may increase rather than decrease the risk of predation of yellow-eyed penguins and other ground nesting birds.

Keywords ferret *Mustela furo*; footprints; grazed pasture; habitat use; predation; rank grass; stoat *Mustela erminea*; yellow-eyed penguin *Megadyptes antipodes*

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INTRODUCTION

Yellow-eyed penguins Megadyptes antipodes are a regionally threatened endemic species, whose numbers are thought to be declining on South Island, New Zealand (Darby & Seddon 1990). Predation by introduced predators such as stoats (Mustela erminea), ferrets (M. furo) and cats (Felis catus) is thought to be a major reason for this decline (Darby & Seddon 1990). Stoats and ferrets were introduced to New Zealand last century to control rabbits (Oryctolagus cuniculus cuniculus) (Gibb & Williams 1990). Although one of their main prey items is rabbits, birds are also an important food source (Marshall 1963; King 1990; Lavers & Clapperton 1990; Smith et al. 1995). Mice (Mus musculus) are also an important prey item for stoats but less so for ferrets and cats (Fitzgerald 1990; Lavers & Clapperton 1990).

Rank grass "buffer zones" have been grown around yellow-eyed penguin breeding areas to protect penguins from predators at Boulder Beach, Otago Peninsula, New Zealand. It was hypothesised that areas of dense ground cover with rank grass and tussock would eliminate access for predators by physically impeding their movement into the breeding colony (Department of Conservation 1991). I have called this the "grass wall hypothesis". Such a bio-control does not require continual intervention and, if effective, would be preferable to expensive trapping programmes currently undertaken to protect the penguins. If such habitat manipulations reduce predation, they have the potential to greatly assist conservation of a whole range of ground dwelling species in New Zealand and elsewhere from introduced mammalian predators.

A radio-tracking study in spring 1993 at Boulder Beach showed that stoats, ferrets and cats all preferred rather than avoided the rank grass buffer zone (Alterio et al. 1998). Potential failure of buffer zones to protect yellow-eyed penguins was further investigated in this study using ink-print tracking rather than radio-tracking. Radio-tracking locates the animals independently from other equipment such as traps or tracking tunnels, but it does not allow the pinpoint accuracy that is achieved with the tracking tunnels. The latter allows the study of the habitat use in great detail, including how the predators move through the buffer zones. Accordingly, this study evaluated the effectiveness of the rank grass zone as a barrier for the stoats and ferrets, and in particular assessed whether tracks through the buffer zone could explain their apparent lack of efficacy. This study also replicates the former study which was conducted in spring and early summer of one year only.

Penguins are flightless seabirds that walk from the beach to their nest site along approximately the same path, thereby creating distinct tracks through the habitat leading directly to nests. Tracks throughout the rank grass may also be used by predators and therefore lead them to the nests with chicks. This study tested the null hypothesis that predators visit nest sites as often as rank grass and tracks; and that they use rank grass as often as tracks.

High relative abundance of favoured prey species such as mice is likely to attract the predators (Alterio 1994). The small mammalian predators may also affect one another's movement. Accordingly I measured the frequency of tracking by mice in different microhabitats and tested whether the presence of stoats or ferrets correlated with mouse distribution; and whether stoats and ferrets used similar or different areas.

STUDY AREA AND METHODS

Tracking tunnels

Tracking tunnels usually deployed to study rodents (King & Edgar 1977; Fitzgerald et al. 1981) were used to study the relative abundance of stoats, ferrets and mice in different habitats during the velloweyed penguin annual breeding cycle. A tracking tunnel consisted either of a round plastic tube (110 mm diameter, 600 mm long); or it consisted of an aluminium cover (600 mm long, 90 mm wide, 120 mm high) over a wooden base (600 mm long, 90 mm wide, 20 mm thick). Both had a metal plate (600 mm long) either inserted into the round plastic tube or lying on the wooden base. This plate was subdivided into three sections: the central one contained a pad soaked with "ink" (120 g polyethylene glycol, 80 g ferric nitrate, 40 g detergent and 30 g water) (King & Edgar 1977); and two outer slots which held chemically treated "tracking paper" (brown paper soaked in 5 % tannic acid in 75 % ethanol) that could easily be removed. A 3 g cube of beef was used as bait, placed in the centre of the ink pad. An animal visiting the tunnel transferred "ink" on its paws to the papers, where it chemically reacted with the tannic acid to produce an indelible print. Papers were replaced (along with bait) weekly.

Placement of tunnels in different habitats

The tracking tunnels were placed throughout yelloweyed penguin breeding areas and adjacent habitats at Boulder Beach (45°50'S, 170°30'E), Otago Peninsula, South Island, New Zealand (Fig. 1), for ten months between June 1993 and June 1994.

Boulder Beach was subdivided into three main habitats: breeding areas, retired pasture and grazed pasture.

Breeding areas: Yellow-eyed penguins present; habitat mainly introduced pasture grasses (cocksfoot (Dactylis glomerata) and Yorkshire fog (Holcus lanatus); sheep and cattle excluded. Four breeding areas were defined: Highcliff (dominated by Hebe elliptica and other native shrubs and some native flax (Phormium tenax); A1 Block (predominantly gorse (Ulex europaeus)); Mid Section and Double Bay (both dominated by flax).

The retired pasture: Yellow-eyed penguins absent; mixed vegetation with macrocarpa trees (*Cupressus* macrocarpa), tree lupin (*Lupinus arboreus*), marram grass (*Ammophila arenaria*) and introduced grass species; sheep and cattle excluded. The essential difference between the retired pasture and the breeding areas is the distribution of yellow-eyed penguins.

Grazed pasture: Yellow-eyed penguins absent; dominated by introduced grass species; grazed by sheep and occasionally by horses.

Placement of tunnels in different microhabitats

Within each breeding area, three microhabitats were defined, in each of which were placed seven tracking tunnels. (1) "Nests" were defined as areas clear of vegetation that had been used as a nest by a penguin pair in the previous summer (1992/93). In most cases they were nest bowls with dropping remains, and were not used again during the 1993/94 breeding season of this study. In the few cases where penguins re-used a nest site with a tracking tunnel, the tunnel was moved 2 or 3 m away. (2) Tunnel sites in "rank grass" were found by throwing random map co-ordinates throughout the breeding areas. (3) "Tracks" were defined as paths of either trampled or shorter grass compared with the surrounding

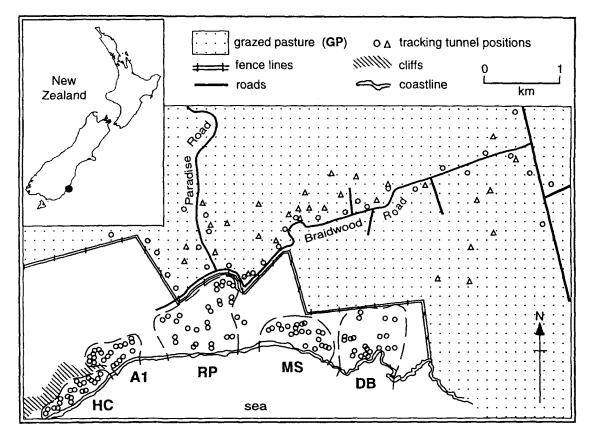


Fig. 1 The relative positions of the yellow-eyed penguin breeding areas, the retired pasture (RP) and the grazed pasture (GP) at Boulder Beach on the Otago Peninsula, Dunedin, New Zealand. The breeding areas include Highcliff (HC), A1 Block (A1), Mid Section (MS) and Double Bay (DB). All indicated positions of the tracking tunnels are approximate only. The positions marked with 0 in the breeding areas and the retired pasture stayed the same throughout the study. In the grazed pasture, the " Δ " symbol mark the positions of the tunnels in June and July 1993, "o" symbol marks the tunnel's positions between September 1993 and May 1994.

grass. These were made by people, penguins, possums (*Trichosurus vulpecula*), and rabbits. "Track" sites were selected as the nearest spot on a track in a random direction (minimum 20 m distance) from a randomly chosen co-ordinate within the study area.

The retired pasture had two types of microhabitat: tracks and rank grass. Fifteen tracking tunnels were distributed on tracks and 15 at random spots in long grass or tall vegetation chosen as described above. Thirty tracking tunnels were placed randomly throughout the grazed pasture surrounding the breeding areas. These positions changed between 26.9.1993 and 4.11.1993 because the land owner did not allow access during lambing. In that period the tracking tunnels were therefore placed in the pasture but close to the road with easy access. The tunnels were moved away from the road at least 10 m into open pasture on 4.11.1993 and their position did not change thereafter. Fig. 1 shows the positions of all tracking tunnels at Boulder Beach.

Identification of prints

Tracking papers were checked independently by two people with the key determined by Ratz (1997) to score presence or absence of each species. Only prints that both observers could agree on were included in the analysis (0.95% of mustelid prints were excluded because it could not be decided whether they were stoats or ferrets).

Seasonal changes in tracking rates

The year was divided into three seasons: winter is defined as the non-breeding period April, May, June and July; spring is defined as the egg and chick guard-stage during October, November and December; and summer is defined as the period of the "post-guard stage" of the chicks in January, February and March. Chicks are most at risk during the mid and late guard phase, November and early December (Darby & Seddon 1990), but some predation in the early post-guard stage in early January has also been recorded (Ratz et al. 1992).

Statistical analysis

Each tunnel was assigned a number, a position (for example, "nest") and habitat (for example, "breeding area"). The proportion of visits by each species was calculated by dividing the number of times one or more footprints of a species was found in the tunnel by the number of times the tunnel was visited per season. This proportion was used for all statistical comparisons, in order to avoid pseudo-replication from wrongly considering each separate visit as being independent of the next.

Non parametric tests (Mann Whitney U and Kruskall Wallis) were used throughout to test differences between microhabitat, area and season in the proportion of times tunnels had been visited by each species. Spearman's rank correlation coefficients were used to test correlations between the proportions of times each tunnel was tracked by stoats, ferrets and mice.

Predator kill trapping

The Department of Conservation operated kill-traps at Boulder Beach yellow-eyed penguin breeding areas and the surrounding grazed pasture from 18 October to 2 November; and 25 November to 17 December 1993, to protect the penguin chicks from stoats, ferrets and cats. "Victor open traps" had a single soft-catch Victor trap (3.7 cm) with bait nailed to tree trunks or on a post above it, and sticks were used to guide the predator over the traps. A plywood cover (59 cm long \times 21 cm wide \times 15 cm deep) was placed over one or two Fenn traps (Mark 4) with bait. Some Timms' traps (a humane kill trap) and gin traps with reversed jaws were also set.

RESULTS

Seasonal changes in stoat, ferret and mouse abundance

The proportion of tracking tunnels with stoat prints varied significantly between the three seasons in all three habitats (Table 1) increasing on average 2.5 times between spring and summer and then decreasing by almost 40% on average between summer and

		All seasons*	Spring vs summer**	Summer vs winter**	Winter vs spring**
All 3 habitats	n	6243	2694	4617	5475
	Stoat	0.000	0.000	0.021	0.001
	Ferret	0.000	0.714	0.000	0.000
	Mice	0.699	0.747	0.308	0.849
Breeding areas	n	3654	1575	2709	3024
	Stoat	0.000	0.000	0.028	0.002
	Ferret	0.000	0.179	0.000	0.000
	Mice	0.067	0.040	0.665	0.053
Retired pasture	n	1314	564	972	1092
	Stoat	0.874	0.713	0.839	0.610
	Ferret	0.002	0.196	0.050	0.001
	Mice	0.519	0.533	0.394	0.335
Grazed pasture	n	1275	555	936	1059
	Stoat	0.009	0.004	0.422	0.012
	Ferret	0.784	0.490	0.546	0.902
	Mice	0.064	0.232	0.489	0.017

 Table 1
 P values for the comparison of overall proportion of visits to tunnels with prints of stoats, ferrets and mice between the three seasons. N is the number of times the tracking tunnels were checked.

* Kruskall Wallis.

** Mann Whitney U test.

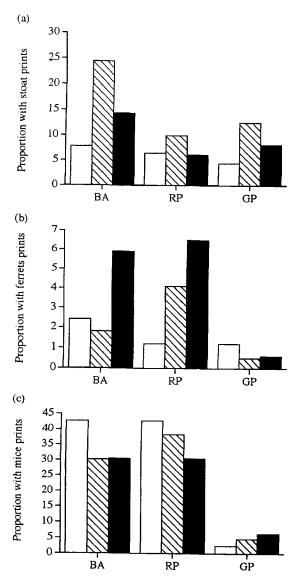


Fig. 2 The proportion of visits to tracking tunnels which found prints of (a) stoat, (b) ferret, and (c) mice. All tracking tunnels in the breeding areas (BA), retired pasture (RP) and the grazed pasture (GP) during spring (\Box) , summer (\boxtimes) and winter (\blacksquare) are pooled.

winter (Fig. 2a). Trapping by the Department of Conservation killed 0 and 25 stoats in October and December respectively, mostly on the border of the retired pasture and the grazed pasture (D. Nelson, pers. comm.). Despite that trapping effort there was a significant increase in stoat prints between spring and summer in the breeding areas and the grazed pasture. The tracking rate also increased then in the retired pasture, but the difference was not statistically significant.

The proportion of tunnels with ferret prints varied significantly between the three seasons in all three habitats, with no change between summer and spring (Table 1), but on average it doubled between summer and winter (Fig. 2b). The Department of Conservation killed two ferrets in each of October and December, mostly on the border between the retired pasture and the grazed pasture (D. Nelson pers. comm.). The tracking rates in the breeding areas declined (but not significantly) between spring and summer, but increased almost 3.5 times in the retired pasture during the same period. Ferrets showed a three and 1.6 fold increase in the breeding areas and the retired pasture respectively (both significant) between summer and winter.

The proportion of tunnels with mouse prints declined by one-quarter between spring and summer in the breeding areas (Table 1; Fig. 2c).

Testing the grass wall hypothesis

To test the grass wall hypothesis the proportion of tunnels with prints at random sites in the rank grass (breeding areas and retired pasture) was compared with the proportion with prints in the grazed pasture. There was a significant increase in use of rank grass in spring by stoats (P = 0.036) and in winter by ferrets (P = 0.0001).

The proportion of tunnels with stoat prints was always higher at the nests than in the grazed pasture (Fig. 3) but these differences were significant only in summer (Table 2). Proportions of tunnels with ferret prints were also always higher at the nests than in the grazed pasture (Fig. 4). These differences were significant in spring and winter and very close to significant in summer, when the effect may have been diluted by the kill trapping of the ferrets (Table 2).

Tracking rates by predators in different microhabitats

The importance of tracks through the rank grass was tested by comparing the proportion of tunnels with prints on tracks compared with the proportion of tunnels set at random positions in the rank grass (in the breeding areas and the retired pasture areas only). There was no consistent pattern in the proportion with stoat prints for either microhabitat (Fig. 3a–c; P = 0.44). In contrast, ferrets were found over five times more often on tracks than in random positions in the rank grass in spring (Fig. 4a; P = 0.004). The tracking proportions were still higher on the tracks

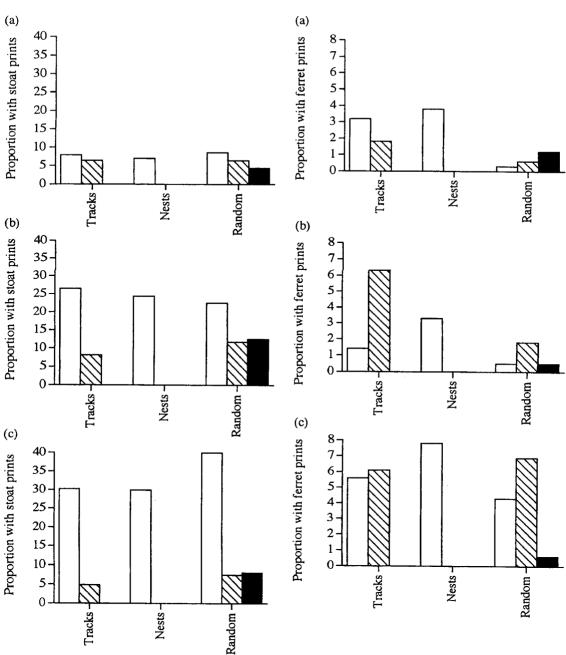


Fig. 3 The proportion of visits to tracking tunnels which found stoat prints in the three microhabitats (tracks, random, nests) in the breeding areas (\Box) , the retired pasture (\boxtimes) and the grazed pasture (\blacksquare) in (a) spring, (b) summer and (c) winter.

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Fig.4 The proportion of visits to tracking tunnels which found ferret prints in the three microhabitats (tracks, random, nests) in the breeding areas (\Box) , the retired pasture (\boxtimes) and the grazed pasture (\blacksquare) in (a) spring, (b) summer and (c) winter.

than in random positions in summer, but this was no longer significant (P > 0.1). In winter, the proportions of tunnels with prints were very similar on tracks and in random positions in the breeding areas and in the retired pasture (Fig. 4c; P = 0.28).

The importance of the nests compared with the tracks was tested only within the breeding areas. A slightly higher proportion of tunnels had stoat prints on the tracks than at nests (Fig. 3a-c), but this was not significant in any season (P > 0.86). There were always more ferret prints in tunnels at nests than on tracks (Fig. 4a-c) but this difference was not significant in any of the three seasons (P = 0.40).

Habitat use by mice

Mice were found significantly more often (P = 0.0001) in the random rank grass positions than in the grazed pasture in all three seasons. Tunnels were tracked by mice over 16 times more often in the rank grass in spring (Fig. 5a), over 11 times more often in summer (Fig. 5b) and over 4 times more often in winter (Fig. 5c).

The microhabitat use in the breeding areas by mice showed no significant difference between tunnels at nests, rank grass and tracks in spring (P = 0.11) and summer (P = 0.83). However, they were found significantly more often at nests in winter (P = 0.0001).

Correlations between occurrences of predators and mice

There were no statistically significant relationships (P = 0.10) between the proportions of visits with stoat cf. mouse prints on tracks, at random positions in rank grass or at nests in any of the three seasons, with the exception of a significant negative correlation amongst tunnels at nests in spring (P = 0.01).

Table 2Comparisons of tracking rates of stoat andferret at nest (breeding areas) compared to at randompositions in the grazed pasture. The p value is the result ofa Mann Whitney U test; the multiplier in brackets givesthe relative increase of tracking rate.

Season	Stoats	Ferrets
Spring	0.176 (1.6 ×)	0.050 (3.2 ×)
Summer	0.029 (1.9×)	0.080 (6.6 ×)
Winter	0.243 (3.7 ×)	0.000 (13 ×)

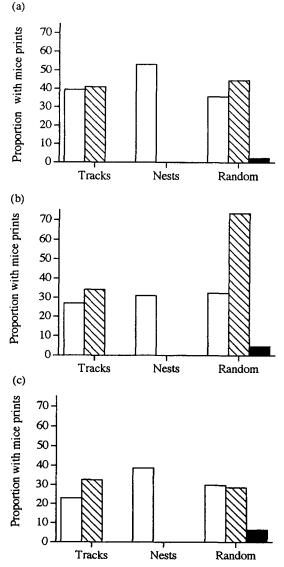


Fig. 5 The proportion of visits to tracking tunnels which found mouse prints in the three microhabitats (tracks, random, nests) in the breeding areas (\Box), the retired pasture (\boxtimes) and the grazed pasture (\blacksquare) in (a) spring, (b) summer and (c) winter.

Similarly, no apparent relationship (P > 0.10) was found between the proportion with ferrets and the proportion with mouse prints, with the exception of a negative correlation between ferrets and mice in random positions in the rank grass in summer (P = 0.04). However, a negative correlation between ferrets and mice in spring was significant (P = 0.058).

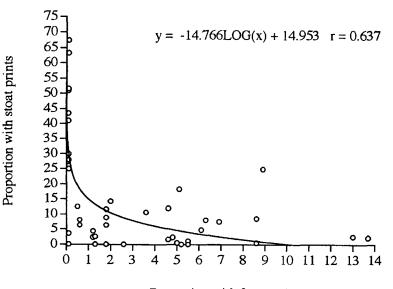
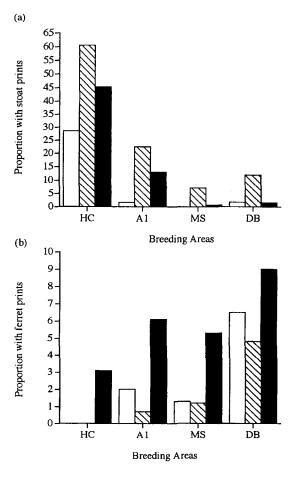


Fig. 6 Scattergram of the proportion of visits recording stoat prints and the proportion recording ferret prints at each tracking tunnel. Each point is the collective results from all tunnels for a given microhabitat, breeding area, retired pasture and grazed pasture, for each seasons (3 microhabitats in 4 breeding areas in 3 seasons, 2 microhabitats in retired pasture in 3 seasons, 1 microhabitat in grazed pasture in 3 seasons; therefore n=45).

Proportion with ferret prints



Do stoats avoid ferrets?

The proportion of stoat prints and the proportion of ferret prints showed a significant inverse relationship (P < 0.001) when the data from all seasons and all microhabitats were included (Fig. 6). In the breeding areas the proportions of visits with stoat prints in all microhabitats was a mirror-image of the proportion with ferret prints (Fig. 7a, 7b). Clearly stoats and ferrets were distributed in quite differently within the study area. Stoats occupied mainly the Highcliff and the adjacent A1 Block, while ferrets were concentrated in Double Bay and the adjacent Mid Section (Fig. 7a, 7b). No significant correlation was found between stoats and ferrets in any of the microhabitats within the rank grass buffer in any season, with the only exception of tracks in summer (Table 3). In spring the correlation between stoats and ferrets is only marginally non-significant (Table 3).

Fig. 7 The proportion of visits to tracking tunnels which found prints of (a) stoats and (b) ferrets in the four breeding areas: Highcliff (HC), A1 Block (A1), Mid Section (MS) and Double Bay (DB) in spring (\Box), summer (\boxtimes) and winter (\blacksquare).

DISCUSSION

Effects of trapping on results

During spring, the Department of Conservation, Otago Conservancy, Dunedin, New Zealand, trapped to kill the predators in the breeding areas and the retired pasture to protect the penguins. Despite the removal of 25 stoats, their tracking rates increased markedly between spring and summer in the penguin breeding areas. In contrast, number of ferret tracks in tunnels decreased slightly between spring and summer in the breeding areas following the removal of four ferrets. This difference between stoats and ferrets was expected because stoats are extremely difficult to catch in spring compared with ferrets (King 1989; Moller et al. 1996). Removal of a high proportion of ferrets may have flattened the differences between grazed and ungrazed sites in late spring and summer, because ferret traps were placed mainly in the latter habitat. Thus, the differences I observed in habitat use by the ferrets would have been even greater in natural conditions unaffected by trapping. Accordingly, measures of differential habitat use in winter or early spring provide the best indications of risk to penguins. Spring is also the time when the chicks are most vulnerable to predators. Newly independent young predators would have appeared from mid summer to autumn.

Test of the grass wall hypothesis

Stoats always concentrated their movements in the breeding areas rather than in grazed pasture. Obviously, the rank grass does not exclude stoats from the breeding areas, but instead attracts them into it. Overseas studies have also found that stoats avoid open spaces and prefer cover from hedgerows,

Table 3Correlations between the proportion of visitswith stoat prints and the proportion with ferret prints ontracks and at random positions (breeding areas and retiredpasture); and in nests (breeding areas). The r value is aSpearman's Rank Correlation Coefficient, and its p valueis given underneath.

	Tracks	Random	Nests
Spring	0.0688	0.9217	0.4495
	(-0.2808)	(0.0152)	(-0.1456)
Summer	0.0437	0.8113	0.8044
	(-0.3112)	(-0.0368)	(0.0477)
Winter	0.2865	0.3199	0.4107
	(-0.1645)	(-0.1535)	(-0.1583)

stonewalls and close ground cover (Erlinge 1977; Sleeman 1989).

Ferrets also always preferred rank grass to grazed pasture, though the difference was significant only in winter. Probably the trapping flattened out differences between the habitats in spring. These results are entirely consistent with and replicate the findings of the radio-tracking studies in spring 1993 (Alterio et al. 1998). Stoats visit other yellow-eyed penguin breeding areas only where there is dense ground cover from rank grass or forest (Moller et al. 1995). This study also confirmed the radio-tracking evidence that predators move deep into the buffer zones, in many cases right to the immediate vicinity of the penguin nests.

To assess the effectiveness of the rank grass buffer as a predation deterrent more completely, tracking rates at nests in rank grass should be compared with tracking rates at nests in grazed pasture. This comparison was not possible because penguins do not nest in the grazed pasture in this study area. Therefore the next best comparison is between the nests in rank grass and random sites within grazed pasture. Stoats were always more often recorded at nests than in the grazed pasture. Nest sites were also preferred by ferrets compared with grazed pasture in spring and winter, and maybe also in summer when the tracking rates were reduced by the kill-trapping of ferrets from the rank grass.

In spring the chance of encountering a ferret at a nest was three times higher than in grazed pasture. This is the extreme minimum measure of the attraction affect of buffers, because ferret numbers were depressed artificially during the kill-trapping in October and December. In winter, ferrets were tracked 24 times more often near the nests than in grazed pasture. Although there are no chicks present in winter, this would still provide a maximum indication of the natural ferret distribution independent of the interference of trapping. Accordingly, growing rank grass around yellow-eyed penguin nests may have increased the chances of chick-ferret encounters by between 3 and 24 times.

The present study and the earlier radio-tracking study (Alterio et al. 1998) concur that the buffer zones do not act like a grass wall to exclude predators.

The importance of tracks

Within the rank grass of the breeding areas and the retired pasture, ferrets visited tunnels set on tracks more than those in random positions in spring and in summer, but not so in winter. During spring and summer the grass stands erect, possibly inhibiting movement through it by ferrets (and probably cats). These large predators are thus channelled down tracks in spring and summer. In winter the grass lies flat, and that may facilitate ferrets' movement in the rank grass areas so that the tracks are no longer preferred.

The nests of the yellow-eyed penguin are always on or at the end of a track, because the adults walk from the sea to the nest to relieve one another's incubation, and to feed chicks. The preference of ferrets for using tracks may therefore increase the risk of predation for the chicks in the nests, because the ferrets' movements are channelled towards the chicks. However, ferrets showed no preference for tunnels near nests compared with those on the tracks, so they may use the nests as part of the track rather than specially investigating them for penguins as prey.

Feral cats are a third predator threatening penguin chicks, but they were not included in this study using small enclosed spaces such as tracking tunnels. During August to October 1992, cats were radiotracked at Boulder Beach and they used the ungrazed areas more than the grazed areas (Alterio et al. 1998). They were also observed on the beach front where they have easy access into the breeding areas along the penguin tracks (Alterio 1994). Cat scats were also found in areas with rank grass (Alterio et al. 1998). Alterio et al. (1998) concluded that the rank grass did not hinder the movements of the feral cats, and I see no reason to suppose that the increased encounter rate between ferrets and penguins due to the rank grass does not also apply to cats.

Relationship in occurrence between predators and their prey

Mice were much more abundant in the rank grass than in the grazed pasture. King et al (1996) also found a significant correlation between mouse abundance and ground cover. This high abundance is one likely reason for the greater use of buffer zones by the predators. Lagomorphs (mainly rabbits, but including hares Lepus europaeus occidentalis), birds and mice were about equally important in the stoat diet around yellow-eyed penguin breeding areas at Boulder Beach between September 1992 and February 1993 (Alterio 1994). The ferret's diet consisted of about equal portions of lagomorphs and birds, with few mice. Lagomorphs dominated the diet of cats with birds and mice about equal in importance. The distribution of mice is expected to be a more important predictor for stoat habitat use than for ferrets and cats and this is broadly corroborated by this study's findings that stoats use rank grass extensively. However, there was no correlation between the tracking rates of stoats and mice in any of the three microhabitats in the three seasons, except for a negative correlation in tunnels at nest sites in spring. Spatial distribution of stoats amongst microhabitats therefore does not follow the distribution of mice, despite the importance of mice in their diet. Similarly ferret distribution did not correlate with mouse distribution within the study area. A North Island study also found that stoats and ferrets did not concentrate disturbed areas with high mouse abundance (King et al. 1996).

However, in the tracking tunnels mice were scored only as present or absent, because it was impossible to determine the number of mice that had visited the tunnel. Therefore, a tunnel with one mouse print was scored the same as a tunnel with many mouse prints. This insensitive measure of the relative abundance of mice means that the lack of correlation between the mouse and predator habitat use must be viewed with caution. The differential use of habitats by stoats, ferrets and cats has been correlated strongly with the abundance of their main prey, in New Zealand and overseas (Erlinge 1977; Pierce 1987; Pascoe 1995). Erlinge (1977) found in Sweden that stoats preferred areas with higher prev density. In the Mackenzie Basin, New Zealand, Pierce (1987) and Pascoe (1995) found cats and ferrets occurred more often in areas with high rabbit abundance. Alterio (1994) came to a parallel conclusion at Boulder Beach, but neither this study nor King et al. (1996) could confirm a correlation between stoat distribution and mouse abundance.

Conservationists had hoped that rank grass buffer zones around nests might decrease the abundance of lagomorphs and thus decreases the abundance of the predators close to penguin nests (Darby & Seddon 1990). However, shelter and food for mice and birds (insects and seeds) are abundant in rank grass (Murphy & Pickard 1990; Alterio 1994; King et al. 1996), and it therefore supports a higher abundance of these species compared with grazed pasture (this study; Alterio 1994). There was no evidence that removal of grazing by stock decreased lagomorph abundance in buffer zones (Bruce 1991; Moller et al. 1995).

Habitat restoration could potentially increase prey abundance by providing food and shelter. Flax, *Hebe ellicptica* and other native shrubs are planted in the breeding areas to provide shelter for penguin nests (Department of Conservation 1991). This vegetation may support a higher prey species abundance, which may have affected the results in this study, because the restoration effort differs between breeding areas in extent and plant species used. A detailed study is required to investigate the effect of habitat restoration with and without exclusion of stock on prey and predator abundance.

Do stoats avoid ferrets and/or cats?

The recorded distributions of stoats and ferrets indicate a possible inverse relationship in occurrence between the two species (Fig. 6a, 6b). Tunnels with high ferret tracking rates had low stoat tracking rates. Ferrets and cats have been reported to kill stoats (Wodzicki 1950; Sleeman 1989) and/or may have deterred, chased away or attacked stoats that established territories within areas frequented by ferrets or cats. Alterio et al. (1998) reported that stoats and ferrets shared common grazed and ungrazed areas at Boulder Beach in August, September and October. However, Pierce (1987) suggested that stoats may have increased after ferret and cat numbers declined after a rabbit poisoning operation in the MacKenzie Basin. Cats also kill stoats (Wodzicki 1950; Gibb & Flux 1973; Fitzgerald & Karl 1979) and they have to be taken into account in the interspecific interactions. Ferrets and cats often occur together (Alterio et al. 1998) so the negative correlation I observed between stoat and ferret occurrence could have been driven by cats and not by ferrets. Alterio et al. (1998) also recorded no cats in Highcliff, and he suggests that the diurnal behaviour of stoats in and around the yellow-eyed penguin breeding areas may have been influenced by the risk of predation from cats and ferrets (Alterio et al. 1998). Alternatively stoats may be actively avoiding areas used by cats or ferrets.

The need for stoats to stay under cover to avoid predation could explain the apparent species separation, but it is also possible that it is caused by different degrees of preference for the foods (insects, mice, birds) concentrated in the ground cover. The almost total lack of a significant relationship between stoat and ferret tracking rates within microhabitats supports this alternative food hypothesis. On the other hand, the lack of correlation could also be due to the small sample sizes. The three predator species have different ecological requirements and they could as well be drawn to different areas independently of each other, as directly interacting. The diet differs between the species and habitats. King (1983) recorded many mice in the diet of stoats from Fiordland beech forest collected through a seedfall cycle, but King et al. (1996) found mostly rabbits, possums, rats (*Rattus* spp.) and birds in the stomachs of stoats from podocarp/mixed hardwood forest in Pureora Forest Park. Ferrets hunted mainly possums and rats at Pureora Forest Park (King et al. 1996), while cats generally concentrated on rabbits (Fitzgerald 1990; Lavers & Clapperton 1990). Highcliff for example has no ferrets or cats, but many stoats. Alterio (1994) found few rabbits and abundant mice, which could explain this distribution of predators. However, the mechanism by which predators influence each other's distribution can be tested only with a reversible selective removal experiment.

Implications for the yellow-eyed penguin management

This and related studies have shown that rank grass does not act as a "grass wall" to exclude predators from yellow-eyed penguin breeding areas. Rather, it attracts them, by increasing the abundance of their prey and/or by providing stoats with cover and shelter from raptors. Ferrets and probably cats are channelled along tracks within the grass to the vicinity of the penguin nests. So all these predators were often found deep within the buffer zones. Both mechanisms increase the chance of predator-chick encounters that may lead to a kill. Tracks can not be removed from the buffer zones because they are needed by the adult penguins. Trapping predators is labour intensive and expensive, and provides only temporary protection for the chicks. Poisoning the predators directly, or indirectly via their prey, could protect the penguins, and trials are being conducted to test the effectiveness of the poison.

This study suggests that habitat manipulations using rank grass buffer zones around yellow-eyed penguins do not protect the penguins and may even make predation worse by increasing the frequency of predator-penguin encounters. Breeding areas within existing rank grass buffer zones should be given added predator control effort; and establishment of new buffer zones should be avoided unless they are needed to establish suitable vegetation for penguin nesting.

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