

NEST-SITE SELECTION BY YELLOW-EYED PENGUINS¹

PHILIP J. SEDDON² AND LLOYD S. DAVIS

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Abstract. Selection of nests by Yellow-eyed Penguins (*Megadyptes antipodes*) is influenced primarily by vegetation. Penguins selected nests with a dense vegetative cover, particularly at 50–100 cm above the ground; nests had a high degree of lateral concealment regardless of the vegetation type. The Yellow-eyed Penguin is a large-bodied penguin breeding in a temperate climate. Overhead vegetative cover provides protection from the sun for both brooding adults and chicks. Lateral concealment due to a solid nest back and surrounding vegetation results in nests that are visually isolated from their neighbors. Internest distances decrease with increasing density of vegetation, reflecting the availability of sites with suitable overhead vegetative cover.

Key words: *Yellow-eyed Penguin; Megadyptes antipodes; nesting habitat; nest-site selection; heat stress.*

INTRODUCTION

Habitat selection results in animals living in a restricted set of environmental conditions (Partridge 1978). Selection of the appropriate environment was once thought to be mediated by the recognition of specific physical features (Hilden 1965), but it is now believed that a sequence of choices is made with various criteria being hierarchically ordered (Klopfer and Ganzhorn 1985). Any demonstration that nest-site selection involves habitat choice must contrast the characteristics of actual nest sites with those of sites available in the surrounding habitat (Burger and Gochfeld 1985). While between-habitat selection may involve a response to some element of general habitat configuration, within-habitat responses may be associated with details of the microhabitat (Klopfer and Ganzhorn 1985). The most common example of microhabitat selection is the placement of nests in dense vegetation, rendering the nest and contents less conspicuous, or offering greater shelter from wind, sun, or nocturnal heat loss (Walsberg 1985).

The traditional nesting habitat of the Yellow-eyed Penguin (*Megadyptes antipodes*) is believed to be coastal forest, with the present day distribution of breeding areas corresponding to the distribution of podocarp/hardwood forests known to be present in pre-European times (Seddon

1988). Logging and land clearance for farming activity has meant that today only isolated patches of regenerating coastal forest persist along the Yellow-eyed Penguin's mainland breeding range. As a result of this breeding Yellow-eyed Penguins are to be found nesting in a variety of alternative vegetation types. With the threat of further habitat deterioration, and gradually declining population numbers (Darby and Seddon, in press), it is essential to determine the factors affecting the selection of nest sites by Yellow-eyed Penguins. Darby (1985) stated that nests almost invariably have a solid back, and that a nesting pair of Yellow-eyed Penguins must be unable to see an adjacent pair. He noted that in the few instances where nests were not visually isolated breeding attempts had failed. No previous quantitative data has been published on the characteristics of Yellow-eyed Penguin nest sites. Here we examine nest-site selection to: (1) determine whether the Yellow-eyed Penguin chooses particular sites, and if so, to identify the important physical characteristics of Yellow-eyed Penguin nest sites; (2) compare nest sites in different vegetation types; and (3) relate nest-site features to the requirements of breeding.

METHODS

STUDY ANIMAL

The Yellow-eyed Penguin breeds only along the southeastern coast of New Zealand's South Island, and in the Stewart, Auckland, and Campbell island groups (Richdale 1957). The adult Yellow-eyed Penguin stands about 70 cm tall and weighs in excess of 5 kg, making it the largest

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² Present address: Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa.

penguin breeding in a temperate climate (Stonehouse 1970). Unlike many other species of penguins, adult Yellow-eyed Penguins may be found at their breeding sites throughout the year with the only true pelagic phase being undertaken by juveniles in their first year.

The Yellow-eyed Penguin is a semicolonial nester. Loose aggregations of nests are enclosed within natural barriers and landing sites, nests are often less than 500 m inland, and are usually situated amongst thick vegetation (Darby and Seddon, in press). The nest itself is a cushion of vegetation in a shallow bowl.

Breeding areas can be characterized by their degree of vegetative cover. Cover is provided by trees, shrubs, or flax growth forms, with densities of nesting birds ranging from $<1/\text{ha}$ to $>6/\text{ha}$ depending on the amount and type of vegetative cover available.

Nest sites begin to be occupied by pairs in June–July, though continuous nest attendance and nest construction does not occur until September. The nest site is occupied constantly from laying in October until the end of the guard phase, a period of about 3 months. During the postguard phase there is a decrease in the use of the nest site as a focal point.

STUDY AREAS AND METHODS

Yellow-eyed Penguin nests were surveyed during the 1986 and 1987 breeding seasons in three areas on the South Island mainland—Highcliff and Boulder Beach ($45^{\circ}5'S$, $170^{\circ}3'E$) on the Otago Peninsula, and Nugget Point ($46^{\circ}2'S$, $169^{\circ}4'E$) in the Catlins. Highcliff (ca. 12 ha, elevation = 40 m) is a densely scrub-covered platform backed by steep cliffs. Boulder Beach (ca. 18 ha, elevation = 40 m) is bordered by low cliffs and grazed pasture. Its vegetative cover is a monoculture of flax (*Phormium tenax*) in dense stands interspersed with open grassy areas. Nugget Point (ca. 12 ha, elevation = 100 m) has a regenerated forest cover of totara (*Podocarpus hallii*) and mahoe (*Melicoytus ramiflorus*) with a scattered understory of ferns (*Dicksonia squarrosa*), marbleleaf (*Carpodetus serratus*), stinkwood (*Coprosma foetidissima*), and nettle (*Urtica ferox*).

The three breeding areas offer three vegetation types (classification after Atkinson 1985): (1) scrub (Highcliff)—woody vegetation dominated by shrubs (stem <10 cm diameter at breast height [dbh]), (2) flax tussockland (Boulder Beach)—tussock growth forms predominate, character-

ized by linear leaves and clumped bases, (3) forest (Nugget Point)—woody vegetation of trees and shrubs (stem >10 cm dbh).

High interest distances and the secretive nature of the Yellow-eyed Penguin makes nest location difficult. Repeated visits to breeding areas ensured that over 90% of the nests were located (based on counts of individuals moving to and from the breeding areas). In some cases the placement of nests under extensive rockfalls made approach impossible. We surveyed nest sites in the scrub and flax areas over two breeding seasons.

For each nest an associated random site was chosen using a table of random numbers for direction (1–8 compass points) and distance (m) from the real site.

A nest area was defined as a 1-m \times 1-m square centered on the nest bowl. At each site, both real and random, we recorded the following: (1) presence or absence of a nest 'back' (a solid obstruction at the immediate base of which the nest bowl is constructed), (2) complete visual isolation from other nests and access paths, (3) percentage vegetative cover, and (4) degree of lateral concealment, measured as the visibility of the nest site when viewed from the side.

Percentage cover is usually not measured precisely, but is estimated visually to the nearest whole number (Barbour et al. 1980). The accuracy of visual estimates of cover may be improved by using small frames, with cover being estimated directly in percent for each placement of the frame, permitting the calculation of an average (Mueller-Dombois and Ellenberg 1974). For estimates of vegetative cover over the nest bowl the nest was divided into four 0.5-m \times 0.5-m squares. Estimates were made for six height intervals 0–10, 10–20, 20–50, 50–100, 100–200, and 200+ cm. Cover estimates were averaged over the four squares to obtain estimates of the percentage cover at each of the height intervals. Total cover in each square was calculated as the mean of the minimum plus maximum cover. Minimum cover was the largest single cover estimate (assuming total overlap between heights), and the maximum cover was the sum of cover estimates at each height interval (assuming no overlap). The average of the summed total cover estimates of the four squares gave a single percentage for total nest cover.

Lateral concealment was recorded as the presence of visual barriers in one to eight octants (45°

arcs) at a distance of up to 1 m from the nest, and at heights of 0.4 m and 0.8 m, being taller than a sitting and a standing Yellow-eyed Penguin, respectively. Internest distances were measured as a straight line between nearest neighbors for all nests found in the three areas. Distances from high tide to the nest bowls were measured in the scrub and flax colonies, by means of a meter wheel run along the penguins' access paths to give a measure of distances actually travelled.

We examined the occurrence of heat stress in Yellow-eyed Penguins by observing banded individuals at marked nests in breeding areas on the Otago Peninsula, between September and November 1985. The proportion of time spent in thermoregulatory behavior was determined by instantaneous scan sampling at intervals of 1 min (Altmann 1974). A total of 5,536 min of observations were made on eight individuals during daylight hours. Daily ambient temperatures were obtained from the Musselburgh Meteorological Station. The accuracy of temperature data was confirmed by recordings made in the field (mean temperature difference $1.4^{\circ}\text{C} \pm 0.9$, $n = 33$ 3-hourly recordings). Thermoregulatory behavior included panting, an upright posture in which the flippers were held out from the sides of the body with flushing of the ventral surfaces evident, and upright restless movements in association with panting.

RESULTS

REAL VS. RANDOM SITES

In scrub the total cover at both real and random sites was greater than 90%, while nests in flax and forest nests had significantly greater total cover than random sites (Table 1). Differences in the amount of cover at different height intervals existed between real and random sites for scrub, flax, and forest (Fig. 1), with nests in all three habitats having significantly more cover than random sites at 50–100 cm. There was no significant difference in the maximum height of vegetation over real and random sites in any of the three habitats (Table 1). Nests only occurred under vegetation with a maximum height of greater than 0.5 m. Both flax and forest nests differed significantly from random sites in the degree of lateral concealment. At heights of 0–0.4 m and 0–0.8 m nests were more concealed than random sites (Table 1). In the more uniform scrub habitat no difference existed in the lateral concealment of real and random sites. There was

no difference between real and random sites in visual isolation from neighboring nests or access paths. All nests were completely visually isolated from adjacent sites, with a high degree of visual isolation occurring at all sites in all habitats. Over 90% of all nests surveyed had some form of solid backing to them. In all habitats at nests there was a significantly greater occurrence of backing than at random sites (χ^2 $df = 1$; scrub $\chi^2 = 11.2$, forest $\chi^2 = 14.7$, $P < 0.001$; flax $\chi^2 = 4.6$, $P < 0.05$). Nests were situated on level ground of greater than 0.3 m area, and in all habitats nests were significantly more often on level ground than were random sites (χ^2 $df = 1$; scrub $\chi^2 = 18.9$, flax $\chi^2 = 20.5$, $P < 0.001$; forest $\chi^2 = 5.1$, $P < 0.05$).

COMPARISON OF HABITATS

Total vertical cover over nests varied from 45 to 100%, with the mean total cover being greatest in scrub and least in forest. The mean maximum height of vegetation was the same in scrub and flax, and tallest in forest. Nearest-neighbor distances varied significantly between the three habitats (Kruskal-Wallis ANOVA, $P < 0.0001$). Internest distances were shortest in scrub, intermediate in flax, and longest in forest (Table 2). Individuals travelled between ca. 40–450 m from high tide to nest sites. There was a significant difference between the scrub and flax breeding areas (Mann Whitney U -test, $P < 0.01$) with birds in the scrub area travelling on average further to nest sites, along access paths crossing steep, open slopes unsuitable for nesting.

THERMOREGULATION

During incubation there was a peak of panting and of upright restless movements occurring in the early afternoon (Fig. 2). The percentage of time spent upright and spent panting increased with increasing temperature ($r = 0.56$, $P < 0.001$; $r = 0.5$, $P < 0.01$). Birds were most often in an upright posture when panting ($\chi^2 = 49.2$, $df = 1$, $P < 0.001$). There was a difference in thermoregulatory behavior between nests, with the frequency of upright restless movements increasing with decreasing degree of overhead nest cover ($\chi^2 = 96$, $df = 2$, $P < 0.001$).

DISCUSSION

A number of factors have been proposed to account for the restricted range of the Yellow-eyed Penguin. Smith (1987) related distribution to oceanographic and climatological features, em-

TABLE 1. Characteristics of Yellow-eyed Penguin nests and random sites in three habitat types.

Habitat	Real ($\bar{x} \pm SD$)	Random ($\bar{x} \pm SD$)	P^a
Scrub ($n = 31$)			
% total cover	93.8 \pm 9.5	90.2 \pm 16.7	ns
Maximum vegetation height (m)	1.6 \pm 0.8	1.4 \pm 0.6	ns
Lateral concealment up to 0.4 m	7 \pm 1	6 \pm 2	ns
Lateral concealment up to 0.8 m	6 \pm 1	5 \pm 3	ns
Flax ($n = 32$)			
% total cover	93.0 \pm 11.5	84.9 \pm 17.0	0.05
Maximum vegetation height (m)	1.6 \pm 0.3	1.4 \pm 0.5	ns
Lateral concealment up to 0.4 m	7.2 \pm 0.9	5.8 \pm 1.5	0.0001
Lateral concealment up to 0.8 m	6.7 \pm 1.2	4.5 \pm 2.0	0.0001
Forest ($n = 17$)			
% total cover	91.1 \pm 15.0	68.1 \pm 28.0	0.01
Maximum vegetation height (m)	3.0 \pm 1.2	2.8 \pm 1.3	ns
Lateral concealment up to 0.4 m	5.1 \pm 1.2	1.9 \pm 2.4	0.001
Lateral concealment up to 0.8 m	4.4 \pm 1.2	1.6 \pm 2.2	0.001

^a Two-tailed Mann-Whitney *U*-test.

phasizing the need for a cool climate. Yellow-eyed Penguins breed south of the 16°C summer isotherm, suggesting that temperatures experienced on land, particularly at nest sites during

the summer, are of major importance in restricting the Yellow-eyed Penguin to the cooler, more southerly regions of the South Island's east coast. Darby and Seddon (in press) have hypothesized that the width of the continental shelf may explain the Yellow-eyed Penguin's absence from areas within the limits imposed by climate, in terms of access to possible year-round feeding grounds at the shelf edge.

The selection of specific breeding areas along the available range may be mediated by physical characteristics. Smith (1987) identifies habitat diversity, slope, and disturbance as factors influencing the selection of a breeding area by Yellow-eyed Penguins. The presence of landing points and access routes inland will limit available areas. Once access inland has been gained a subset of physical characteristics may then be chosen. The presence of small areas of level ground in conjunction with vegetative cover is probably the primary characteristic governing the choice of a breeding area. The diversity of plant types utilized by Yellow-eyed Penguins suggests it is not the species so much as the growth-form and its association with level ground that determines its suitability as a nest site.

Within a chosen breeding area details of the microhabitat are used to identify specific nesting sites. This study has identified two principal features of Yellow-eyed Penguin nests: lateral concealment and overhead cover.

LATERAL CONCEALMENT

Yellow-eyed Penguin nest sites are usually visually isolated from neighboring sites. Visual iso-

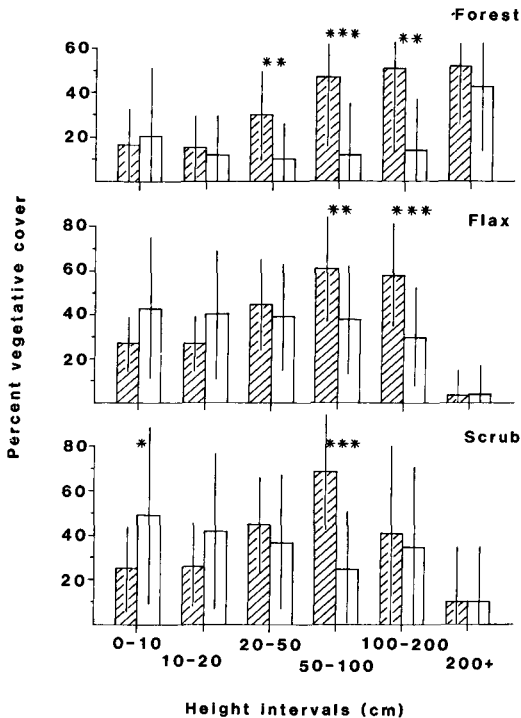


FIGURE 1. Percent vegetative cover ($\bar{x} \pm 1$ SD) at different heights over Yellow-eyed Penguin nests (shaded bars) and random sites (open bars) in three habitats. Mann-Whitney *U*-test, two-tailed; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

TABLE 2. Internest distances and distances from nests to the sea in three Yellow-eyed Penguin breeding habitats.

	Scrub	Flax	Forest
Nearest-neighbor distance (m)			
$\bar{x} \pm SD$	11.6 \pm 6.0	16.2 \pm 12.7	31.8 \pm 17.1
Range	4.6–23.6	4.6–61.0	13.8–78.0
<i>n</i>	37	32	17
Distance to the sea (m)			
$\bar{x} \pm SD$	202.6 \pm 107.7	124.2 \pm 100.7	—
Range	48–345	44–444	—
<i>n</i>	53	32	—

lation results from the high degree of lateral concealment provided by the surrounding vegetation and the nest back. Over 90% of the nests surveyed in all areas had some sort of solid back to them. Nest backs may be vegetation stems, fallen logs, embankments, or rocks. Lateral concealment of nests becomes most evident in habitats with a variable cover below 1 m in height. In flax and forest, nests were more concealed than random sites, while in scrub the dense vegetative cover meant that both real and random sites were well concealed.

Concealment of nests has been related to protection from predation. The selection of sites in dense vegetation as an antipredator strategy has been shown for several birds (Hines and Mitchell 1983, Burger and Gochfeld 1986, Goransson and Loman 1986, Tidemann and Marples 1988). Feral cats and mustelids are the major terrestrial predators of Yellow-eyed Penguin chicks throughout their range. A high density of vegetation surrounding the nest may inhibit predator access. However, dense vegetation throughout a breeding area, rather than immediately around a nest, is more effective at hindering predator movements between nest sites (Seddon 1988).

The denser the vegetation the closer the internest spacing, thus forest which is largely open beneath the canopy has the highest internest distances. It is likely that nest spacing is related to the availability of suitable vegetative cover with high nest concealment, and therefore visually isolated sites are a consequence of this.

OVERHEAD COVER

All nests surveyed in the three breeding areas were under some degree of overhead vegetative cover. The total percent of vegetative cover over nests was often similar to that over random sites, however, the vertical distribution of the cover was very different. Random sites often had dense

ground-level cover, while nests were placed in areas clear of plant stems or rocks, but with a high degree of cover particularly between 50–100 cm above the ground.

To counter heat loss in water, penguins have thick layers of subdermal fat and dense, waterproof plumage. As a consequence penguins tend to be over insulated on land. Despite physiological mechanisms promoting heat loss on land, even moderate ambient temperatures and a high

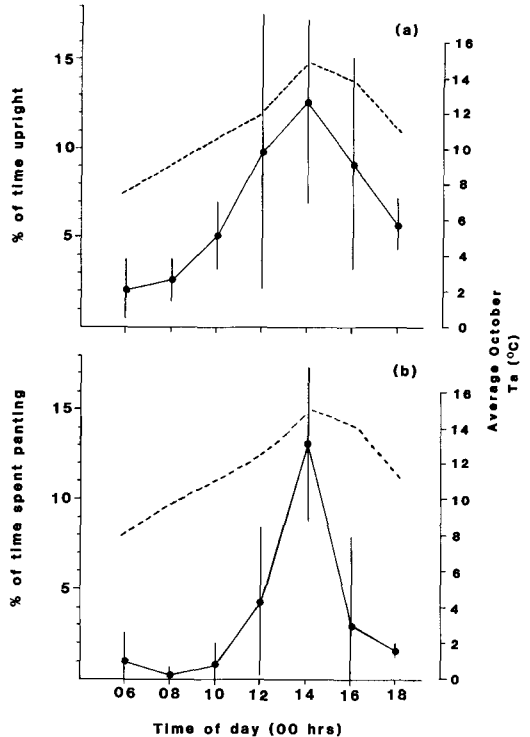


FIGURE 2. Proportion of time spent by incubating Yellow-eyed Penguins in: (a) upright restless movements, and (b) panting ($\bar{x} \pm 1 SD$) by time of day. Dotted lines indicate mean ambient temperatures.

incidence of solar radiation may result in heat stress (Frost et al. 1976). Only during incubation is the Yellow-eyed Penguin tied to one particular area, in a prone posture for the whole day. In the prone posture the feet are covered and therefore inefficient as thermal radiators. The flippers are of limited use as heat-loss surfaces as they can only be extended to the sides, remaining close to the ground and often sheltered from breezes by the material of the nest. In order for an incubating bird to lose excess heat it must pant and adopt a more upright posture. Temperatures reach a maximum in early to mid-afternoon at which time there was a peak in upright restless movements and a peak in the frequency of panting. Yellow-eyed Penguins at sparsely covered nest sites suffer more from heat stress than birds at well-shaded nests. Overheating and the need to pant may represent a significant energy drain for the fasting bird. We have observed heat-stressed Yellow-eyed Penguins deserting their nests in search of nearby shade. Galapagos Penguins (*Spheniscus mendiculus*) incubating at exposed nests may also desert their eggs when the solar radiation becomes too great (Boersma 1975). The adoption of an upright posture exposes the clutch to ambient temperatures, while an increase in the frequency of upright restless movements will increase the possibility of accidental ejection of eggs from the nest bowl.

Chicks too are subject to overheating. Between about 1 and 9 weeks old the chicks are covered with a dense grey down. On hot days chicks seek shade under vegetation. At sparsely covered nests in open pasture chicks will stand or lie in nearby streams or swampy ground on hot days (Seddon, in press). Some chicks have died as a result of heat stress at exposed nests (J. Darby, pers. comm.).

Heat stress during incubation has been observed in some Northern Goshawks (Reynolds et al. 1982, Speiser and Bosakowski 1987), gulls (Dawson et al. 1976, Bartholomew and Dawson 1979, Hand et al. 1981), and penguins (Stonehouse 1970, Muller-Schwarze 1984). The use of cover at the nest site as protection from the sun has been recorded in several birds (Howell and Bartholomew 1961, Fogden 1964, Burger 1981, Clark et al. 1983, Burger and Gochfeld 1986, Goransson and Loman 1986). Penguins of the *Eudyptula* and *Spheniscus* genera breed in temperate to tropical climates. Members of these genera are burrow nesters, a strategy believed to

allow individuals to avoid insolation during breeding (Stonehouse 1970). The traditional coastal forest nesting habitat of the Yellow-eyed Penguin would have provided a cool environment for the activities of breeding. With the loss of this type of cover the Yellow-eyed Penguin, with dense waterproof plumage and subcutaneous fat, finds itself overinsulated on the land, forced to seek alternative habitats which provide some degree of overhead cover and therefore protection from the sun.

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