Selection for protection from insolation results in the visual isolation of yellow-eyed penguin *Megadyptes antipodes* nests

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Summary

The concealed and widely dispersed nests of the rare and endangered yellow-eyed penguin *Megadyptes antipodes*, or "hoiho", have been considered to reflect an essential requirement of the visual isolation of nest sites from conspecifics. However, this may be a consequence of selection for habitat features that provide protection from insolation, thereby minimising the risk of heat stress. We aimed to determine whether visual isolation from conspecifics or protection from insolation is the primary driver of hoiho nest site selection, in order to improve the understanding of hoiho nesting requirements and the effectiveness of habitat restoration. We compared the mean maximum distance of visibility and the mean % of insolation cover (derived from measurements of diffuse non-interceptance) of active nests with randomly sampled unused sites in flax and coastal scrub at Boulder Beach, and in coastal forest at Hinahina Cove, New Zealand, 2006 - 2007. Univariate ANOVA and Mann-Whitney tests, and the evaluation of logistic regression models with Akaike weights, indicated that the amount of insolation cover was more important than visibility in hoiho nest site selection. In addition, Spearman's correlations indicated that decreasing insolation cover significantly increased the visibility of nests in the forest habitat, and had a similar effect on inter-nest distance in flax. We infer that hoiho nest site selection and distribution are influenced primarily by the location and density of micro-habitat features (particularly within 1 m of the ground) that provide optimal protection from insolation. Strong selection for these features consequently results in the typical but non-essential visual isolation of nest sites from conspecifics. We recommend that restoration initiatives aim to produce structurally diverse nesting habitats with sub-canopy vegetation densities varying at different heights (50 – 100 cm above ground may be most important).

Introduction

For many birds, reproductive success is dependent on the selection of a suitable nest site. Common factors that define a suitable nest site may include: shelter from adverse climatic conditions, protection from predation, presence of conspecifics, minimised disturbance, and/or proximity to food (Partridge 1978, Cody 1985, Walsberg 1985, Kim and Monaghan 2005). In a given habitat, cues to the locations where suitable nesting conditions could be met are often provided in certain features, such as vegetation composition and/or structure (Partridge 1978, Cody 1985). Identifying and understanding the factors that are most important, and the habitat features that provide them, are essential to the success of species-targeted habitat restoration initiatives.

The endangered yellow-eyed penguin *Megadyptes antipodes*, or "hoiho", inhabits a restricted range in New Zealand (McKinlay 2001, Birdlife International 2012). Throughout the South Island part of the hoiho's range, most of the coastal forest habitat that existed before European settlement has been cleared (Seddon and Davis 1989, Darby and Seddon 1990). As a consequence, hoiho breeding in this area nest primarily in alternative habitats that may reduce reproductive success (Darby and Seddon 1990). This issue has been addressed by the New Zealand Department of Conservation and the Yellow-eyed Penguin Trust, both of which identify the re-vegetation of nesting habitats as a primary management activity, and one of nine objectives in the "Hoiho recovery plan" (McKinlay 2001, Yellow-eyed Penguin Trust 2012).

Similar to other penguin species at temperate latitudes, hoiho nest primarily in locations that are sheltered from direct exposure to sunlight, which is considered to reflect a strategy for avoiding negative effects that can result from insolation (Stonehouse 1970, Seddon and Davis 1989, Darby and Seddon 1990, Williams 1995). However, unlike other penguins, hoiho nests are typically well concealed and widely dispersed, with an average inter-nest distance that can exceed 20 metres (Seddon and Davis 1989, Darby and Seddon 1990, Marchant and Higgins 1990, Moore 1992). This results in the common visual isolation of each nest, which has been consistently documented (e.g. Richdale 1957, Seddon and Davis 1989, Marchant and Higgins 1990, Moore 1992), and is considered to be an essential requirement for hoiho (Darby 1985, McKinlay 2001, Birdlife International 2012). Darby (1985) and Lalas (1985) reported observations of nest failures that appeared to result from a lack of visual isolation from conspecifics. However, Seddon and Davis (1989) considered that the visual isolation of nests from conspecifics may only be a consequence of hoiho selecting sites with substantial cover that provides ample protection from insolation.

Visual isolation from conspecifics has been observed to positively affect the breeding performance of *Larus* gulls. For example, Burger (1977) and Kim and Monaghan (2005) observed shorter inter-nest distances and greater reproductive success for gulls that nested in vegetation as opposed to bare ground. This correlation was partially attributed to the lower visibility between nests in vegetation, which reduced the frequency of aggressive interactions and other disturbances between neighbours, and therefore allowed incubating birds to spend more time resting and attending offspring (Burger 1977, Bukacińska and Bukaciński 1993, Kim and Monaghan 2005).

Determination of whether visual isolation from conspecifics or protection from insolation is the primary driver of hoiho nest site selection has important implications for on-going habitat restoration that seeks to maximise nesting densities. If visual isolation from conspecifics is an essential nest site requirement for hoiho, then, similar to *Larus* gulls, the availability and distribution of suitable sites in a nesting habitat could be influenced by the distance of visibility. However, if visual isolation is a result of selection for adequate shelter from insolation, then nest site selection and distribution may be influenced by the density or distribution of habitat features that provide a suitable amount of protective cover from sunlight. Previous studies have recorded whether hoiho nest sites were visually isolated from each other (e.g. Seddon and Davis 1989, Moore 1992), or derived an index of visual isolation based on the density and cover of vegetation at nest sites (Smith 1987). Here we present a study that assessed whether the apparent importance of visual isolation from conspecifics could be determined by comparing the distance of visibility of active nests with unused sites, and also whether inter-nest distance correlated with the distance of visibility. To assess whether visual isolation is a consequence of selection for adequate protection from insolation, we compared the amount of cover from insolation at nests with that at unused sites, and tested for correlations of this variable with the distance of visibility and inter-nest distance. Our aim was to advance the understanding of hoiho nest site requirements, and subsequently contribute to improving the effectiveness of habitat restoration and re-vegetation activities.

Methods

Study areas

We examined hoiho nest site selection and distribution in three habitat types at two study areas on the southeast coast of the South Island of New Zealand: flax and coastal scrub at Boulder Beach, and coastal forest at Hinahina Cove (Figure 1). Boulder Beach comprises c. 55 ha of vegetated land extending up to 250 m inland and situated along c. 2 km of mixed gravel-sandy beach and some cliffs on the south coast of the Otago Peninsula. The area was used for sheep grazing until the mid-1980s when it was fenced and a re-vegetation programme was established (Seddon *et al*. 1989). Vegetation cover consists of varying patches of a native coastal scrub (*Hebe elliptica*) and flax (*Phormium tenax*) interspersed amongst larger areas of grasses (mainly *Ammophila arenaria* and *Poa* species) and exotic scrub species (primarily *Lupinus arboreus* and *Ulex europaeus*). Also present are small patches of native broadleaf trees (*Cordyline australis* and *Myoporum laetum*), shrubs (e.g. *Solanum laciniatum*), vines (e.g. *Muehlenbeckia australis*), bracken fern *Pteridium esculentum*, and rushes. The flax habitat was dominated by *Phormium tenax*, and included occasional *Hebe elliptica* scrub, *Solanum laciniatum*, *Blechnum* fern species, and grasses. Scrub habitat consisted primarily of *Hebe elliptica* and/or exotic *Ulex europaeus*, and also included some *Myoporum laetum*, *Lupinus arboreus*, *Muehlenbeckia australis*, and *Solanum laciniatum*. The flax and scrub habitats at Boulder Beach were mapped using orthorectified colour aerial photographs taken in September 2006, and validated with observations recorded during data collection.

Hinahina Cove is c. 100 km south-southwest of Boulder Beach and has a rocky coastline along sheer cliffs. Hoiho access the area via a rock platform at the mouth of Hinahina Stream and nest within native coastal forest that extends c. 2 km inland along the stream and on a steep slope to the north. Open grazed pasture lie on a gradually rising slope to the south of the stream. The forest covers c. 565 ha, yet the area used by hoiho for nesting is considered to be c. 25 ha (Seddon et al. 1989). The forest canopy consists of *Melicytus lanceolatus*, *Weinmannia racemosa*, and *Myoporum laetum* near the coast, changing inland to podocarp tree species such as *Metrosideros umbellata*, *Podocarpus ferrugineus*, and *Dacrydium cupressinum*. Much of the area beneath the forest canopy is relatively open, which may be partly due to cattle grazing that occurred until 1987, when the area was designated a reserve (Seddon *et al*. 1989), and may also reflect the presence of deer and pigs (New Zealand Department of Conservation 2013). Nevertheless, crown ferns *Blechnum discolor* cover much of the forest floor, and other scattered patches of sub-canopy vegetation consist of broadleaf trees (e.g. *Griselinia littoralis*, *Myrsine australis, and Pseudopanax crassifolius*), fern trees (e.g.

Dicksonia species), the liane *Ripogonum scandens*, and shrubs (e.g. *Coprosma* species). Logs, stumps and snags of dead or fallen trees are also scattered throughout the forest.

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Data collection

The study areas were thoroughly searched for active nest sites beginning in October 2006, and periodically throughout the breeding season, until January 2007. Active nest site locations were recorded with a professional grade GPS (Leica Geosystems GS20 Professional Data Mapper), with which we obtained a sub-metre level of accuracy following the differential correction of coordinates. At Hinahina Cove we examined all 14 active nest sites found, whilst at Boulder Beach, the number of examined nest sites was limited to 31 of the 55 found because of resource and time constraints, the difficult accessibility of some nests due to cliffs or steep, slippery slopes, and the exclusion of two nests located in man-made structures (i.e. a nest box and the remnants of a small stone hut).

We established locations of unused sites to compare with active sites in each habitat using a random point generating algorithm in a GIS, excluding points that occurred within 5 m of each other or an active nest site (based on the minimum distance between nests reported by Seddon and Davis (1989)). When in the field, if the randomly generated location of an unused site did not occur on level ground, or occurred outside of the designated habitat type (e.g. in an open, un-vegetated or grass covered area), then the position of the site was relocated to within the nearest habitat patch matching the designated type (flax, scrub, or forest). Table 1 provides a summary of the number of active nest and random unused sites examined in each habitat type.

To minimise disturbance to breeding adults and chicks, we collected measurements of the mean maximum distance of visibility (hereafter referred to as "visibility"), and the mean amount of protection from insolation (“insolation cover”) of active nests and unused sites in February 2007, when nests had been recently vacated. For the assessment of visibility, we assumed that human vision was not significantly different than hoiho vision on land. This was based on findings that penguin visual acuity appears to be nearly emmetropic in air (Sivak and Millodot 1977, Sivak *et al*. 1987), and the physiology of the penguin retina is considered well adapted to the spectral properties of both deep water and terrestrial environments (Bowmaker and Martin 1985, Suburo and Scolaro 1999). We assessed visibility with a profile pole, an effective device for measuring the amount of visual obstruction of vegetation and/or other habitat structures (Robel *et al.* 1970, Griffith and Youtie 1988, Higgins *et al.* 1996). We used a profile pole constructed of a 100 cm by 5 cm plastic tube divided into ten alternating black and white sections, and fitted with a metal spike in a cap on the bottom to anchor it in the ground. At each active and unused site, we placed the pole in the centre and, at the height of a standing adult hoiho (approximately 60-65 cm based on Darby and Seddon (1990) and Marchant and Higgins (1990)), we recorded measurements of the percentage of each 10 cm section of the pole visible from set distances along three bearings. The first bearing was determined by a random number between 0-359, and the second and third bearings were 120 degrees to the east and west of the first bearing. Along each bearing we measured visibility beginning at 0.5 m from the pole, then at 1 m, 2 m, and every subsequent 2 m until less than five percent of the pole could be seen. We defined the maximum distance of visibility as the set distance immediately preceding that where less than 5 percent of the pole was visible. We therefore collected three measurements of the maximum distance of visibility at each site, one for each bearing, and used the mean of the three measurements in analyses. The top 20 cm of the pole were excluded from the assessment as this portion extended above the canopies of several sites.

To assess the amount of insolation cover of active and unused sites, we used the LAI-2000 Plant Canopy Analyser (LI-COR Inc. 1990) to obtain estimates of the fraction of gaps in site canopies. The LAI-2000 estimates parameters of canopy structure by comparing measurements of diffuse solar radiation recorded in a nearly hemispheric “view” (i.e. both overhead and laterally) above (or outside) and beneath a canopy (LI-COR Inc. 1990, Welles and Norman 1991). An estimate of the fraction of gaps in a canopy is obtained with the diffuse non-interceptance parameter ($\boldsymbol{\tau}$), which is the probability of diffuse radiation above a canopy penetrating to a particular location beneath the canopy (LI-COR Inc. 1990, Welles and Norman 1991). At each active and unused site, we collected one above-canopy recording and a set of three beneath-canopy recordings taken approximately 10 cm above the ground at the same position near the centre of the site. We captured above-canopy recordings of the open sky for sites in the flax and scrub habitats at Boulder Beach, whilst at Hinahina Cove we captured above-canopy recordings beneath the main forest canopy, which we considered to be continuous and uniform. The LAI-2000 divided the average of the beneath-canopy recordings by the above-canopy recording to obtain a single $\boldsymbol{\tau}$ value that ranged from 0 (no gaps in the site canopy = assumed complete insolation cover) to 1 (little or no site canopy = assumed minimal insolation cover) (LI-COR Inc. 1990). For example, a $\boldsymbol{\tau}$ value of 0.47 would indicate gaps in an average of 47 % of a site canopy (LI-COR Inc. 1990), which we would assume to indicate approximately 53 % insolation cover. Subsequently, for data analyses we converted $\boldsymbol{\tau}$ to % insolation cover (i.e. 100 * (1 - $\boldsymbol{\tau}$)).

Data analysis

Comment [RC2]: Table 1 can be placed before this sub-section, or as soon as possible after the end of the Data Collection sub-section (e.g. top of next page).

To assess the relative importance and potential interaction and/or correlation of visibility and insolation cover, we conducted a three-part analysis that included univariate, logistic regression, and correlation components. The sample sizes for these analyses were determined after excluding outlying values that had a significant effect on the distribution and variance of a data set (defined by habitat and site type, e.g. forest habitat - active sites; Table 1).

For the first analysis component, we used univariate ANOVA and Mann-Whitney tests (for non-normally distributed data sets) to separately compare the mean visibility and % insolation cover recorded for active sites with the mean values recorded for unused sites in each habitat, and to compare habitats in terms of the means of each variable recorded for active sites. However, we did not compare the mean % insolation cover at forest active sites with that at flax and scrub active sites due to the different conditions in which above-canopy measurements were recorded. To further test the significance of any differences, we compared the means of the observed data with five thousand bootstrap samples of each data set.

Logistic regression analysis has been recommended for evaluating multiple variables in comparisons of used (i.e. active nests) and available (i.e. random unused) units (Manly *et al*. 2002). Therefore, for the second analysis component, we assessed binary logistic regression models containing different combinations of the descriptive variables (i.e. visibility, % insolation cover, and an interaction), with a binary dependent variable of 1 = nest site, or 0 = unused site. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c), and particularly the Akaike weights (w_i) to evaluate the relative likelihood and support of each model (Burnham and Anderson 1998, Johnson and Omland 2004, Wagenmakers and Farrell 2004). For the third analysis component, we evaluated Spearman's correlations between the visibility and % insolation cover of active sites in each habitat.

For the analysis of inter-nest distance, we used a GIS to obtain Euclidean distances (to the nearest 0.1 metre) between the differentially corrected GPS recorded locations of active sites. To avoid effects resulting from the fragmented distribution of the flax and scrub habitats at Boulder Beach, we limited the inter-nest distance samples of these habitats to include only values for active sites that occurred within the same contiguous habitat patch (Table 1). We used Mann-Whitney tests to compare the mean minimum inter-nest distances in each habitat type, and we used Spearman's correlation to assess the effect of visibility and % insolation cover on inter-nest distance in each habitat.

Results

The univariate analysis revealed varied yet significant differences between active and unused sites in all but one comparison. In the assessment of visibility, unused sites in forest were visible from a mean maximum distance of 4.2 m, which was greater than the mean visibility of active sites by more than 2.5 m ($F = 26.4$, $P < 0.001$, Figure 2). At Boulder Beach, the mean visibility of unused sites in scrub was greater than that of active sites by 0.9 m ($F = 4.2$, $P = 0.05$), while in flax the mean visibility of active and unused sites was nearly equal (Figure 2). In habitat comparisons, active sites in forest were visible from a mean maximum distance that was 0.8 m greater than that of active sites in flax ($U = 45.5$, $P < 0.01$) and scrub ($F = 5.1$, $P = 0.03$), which were not significantly different in visibility (Figure 2).

As with visibility, the difference between active and unused sites in % insolation cover was again greatest in the forest habitat, where the mean diffuse non-interceptance values indicated an average % insolation cover at active sites that was 35 % greater than at unused sites ($U = 10.0$, $P < 0.001$, Figure 3(a)). The mean diffuse non-interceptance values recorded in flax and scrub habitats indicated a relatively high % insolation cover at both active and unused sites. However, the average % insolation cover at active sites was greater than at unused sites by a relatively small yet statistically significant 5 % in both flax (F = 5.9, P = 0.02), and scrub (F = 15.4, P = 0.001, Figure 3(b)). Similarly, in a comparison between active sites in scrub and flax, the average % insolation cover at scrub sites was greater than at flax sites by 5 % (U = 50.0, $P < 0.001$, Figure 3(b)).

According to the Akaike weights (w_i), no single model in the logistic regression analysis exhibited a particularly strong likelihood. However, for each habitat, the single model with the greatest w_i reflected the univariate analysis results, i.e. both visibility and insolation cover were important in forest (w_i = 0.49) and scrub (w_i = 0.72) while only insolation cover was important in flax (w_i = 0.58; Table 2). When considering the sum of the two or three greatest w_i (i.e. $\sum w_i$), it appeared that an interaction of visibility and % insolation cover was likely in all three habitats, and that % insolation cover was potentially more important than visibility in flax and scrub. For example, in scrub habitat the interaction model and the model containing both variables had a $\sum w_i$ of 0.92, and the visibility model w_i = 0 (Table 2).

Similarly, the results of the correlation analysis also suggested an interaction effect of visibility and % insolation cover on hoiho nest site selection. This was apparent in forest, where the only significant Spearman correlation indicated that a decrease in % insolation cover had a relatively strong, positive monotonic effect on the visibility of active sites (r_s = 0.66, P = 0.02, Figure 4(c)).

Mean minimum inter-nest distance was greatest in forest (23.4 m), but not significantly greater than in scrub (22.6 m), whereas mean minimum inter-nest distance in flax (10.7 m) was significantly less than in forest (U = 10.0, $P < 0.001$) and scrub (U = 4.0, $P < 0.001$). The assessment of Spearman's correlations between minimum inter-nest distance and each of the two variables in each habitat revealed a moderately strong, positive monotonic influence of decreasing insolation cover on minimum inter-nest distance in the flax habitat (r_s = 0.63, P = 0.03, Figure 5(b)).

Discussion

We examined hoiho nest site selection and distribution in three habitats with different structural and vegetation compositions and densities. The differences between the habitats, particularly the structure and density of vegetation within 1 m of the ground, were clearly reflected in the results of our analyses. For example, the greatest mean visibility observed in the forest habitat at Hinahina Cove reflected the low density of ground level (i.e. up to 1 m) vegetation relative to scrub and particularly flax, where the nearly equal visibility of active and unused sites reflected a consistently high density of ground level vegetation cover.

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Despite the variation between habitats in our results, there was greater and more consistent support for the importance of the amount of insolation protection in hoiho nest site selection. While we observed a great difference in the visibility of active and unused sites in forest, and also a significant difference in scrub, this did not reflect an importance of visual isolation from conspecifics in hoiho nest site selection. We propose at least three reasons for this: 1) there was a clear interaction/correlation between visibility and insolation cover in forest and scrub (and potentially in flax), 2) there was no correlation of inter-nest distance with visibility, and 3) there appeared to be a strong correlation of inter-nest distance with the amount of insolation cover, at least in flax. Subsequently, our results provide stronger support for the hypothesis that the visual isolation of hoiho nests from conspecifics is at least partly a consequence of selection for nest site features that provide significant protection from insolation.

Like all penguins north of the sub-Antarctic, the hoiho is considered to be over-insulated for the terrestrial environment, and subsequently may require shelter from insolation while on land to avoid heat stress (Stonehouse 1970, Seddon and Davis 1989). Protection from insolation may be most important during the breeding season, when incubating birds are particularly prone to heat stress (Frost *et al.* 1976, Seddon and Davis 1989). Therefore, for hoiho, the most important features of a nest site would appear to be those that help minimise the risk of negative effects resulting from insolation.

Hoiho indeed appear to be highly selective of the amount of cover at a nest site, particularly within 50 – 100 cm of the ground regardless of the habitat type (Seddon and Davis 1989). This was particularly evident in the forest habitat at Hinahina Cove, where, despite the apparently low risk of insolation due to the intact forest canopy, hoiho primarily selected maximally sheltered nest sites that were often in hollows under logs, stumps, or tree stems. This has also been observed on New Zealand's southern islands, where hoiho nesting areas are covered primarily by indigenous coastal scrub (e.g. as described for Campbell Island by Moore (1992)). The hoiho's selection for nest sites with these structural features can be considered analogous to the use of caves and burrows by other penguin species at temperate latitudes (Stonehouse 1970, Frost *et al.* 1976, Williams 1995). Along with insolation protection, these sites would also offer shelter from other climatic effects, thereby providing a moderate and stable micro-climate. The selection for these types of sites could also explain the use of a wooden nest box and stone hut remnant we observed (but excluded from analyses) at Boulder Beach. Furthermore, a study on the deployment of nest boxes designed after these typical features of hoiho nest sites showed that they were readily and successfully used by hoiho (Lalas et al. 1999).

In contrast, McKay et al. (1999) observed hoiho successfully nesting in a grazed grassland-dominated habitat, where a few nests had little to no overhead and lateral cover. The authors of this study did not specifically state whether hoiho at these nest sites were visible to each other. However, they did report that the grassland nests had a lower success rate than nests in adjacent shrubland habitat, which they considered likely to reflect the grassland nests had been established by inexperienced breeders (McKay et al. 1999). Two important features of the most exposed grassland nest sites observed by McKay et al. (1999) were a solid backing in the form of a clay bank, rock, and rushes, and a south facing aspect. McKay et al. (1999) reported that the uncovered nest sites with a south facing aspect were probably not affected by insolation as they were only exposed to sunlight during early morning hours. Marchant and Higgins (1990) also reported observations of hoiho nesting on steep cliffs that faced away from the sun and toward the sea. A solid backing structure has been reported as an important feature of hoiho nest sites by Seddon and Davis (1989), who observed that active nest sites had a backing structure significantly more often than random unused sites in all habitats examined. While we did not assess the significance of a solid backing structure, the likely presence of this feature at active nest sites may have influenced the results of the visibility and insolation cover analyses. In the flax and scrub habitats, the relatively small yet significant difference between active and unused sites in the amount of insolation cover may have reflected a greater occurrence of a solid backing structure at active nest sites.

Along with the consequence of visual isolation, the relatively large distances between hoiho nests can also be at least partially attributed to the selection for structural micro-habitat features that provide extensive cover within 1 m above the ground. This was reflected in the significant correlation results, particularly for flax habitat, where inter-nest distance in flax appeared to be strongly influenced by the amount of insolation cover. This and the influence of insolation cover on the visibility of nest sites in forest indicated that a lower ground-level (i.e. up to 1 m) vegetation density could result in a lower density of sites with a suitable amount of cover, and therefore a greater distance between nests. In any nesting habitat, the availability and distribution of suitable nest sites will be influenced primarily by the spatial variation of the preferred features. For example, the distribution of nests in forest habitat may reflect the spatial distribution of logs, stumps and similar features containing the hollows that hoiho seem to prefer. Habitats that do not contain these particular features, yet consist of relatively dense vegetation within 1 m of the ground, may provide suitable nest sites at shorter distances and greater densities. This was apparent in the flax habitat we examined at Boulder Beach. However, we cannot infer from this observation that a nesting habitat dominated by flax may be more suitable for hoiho than other habitat types. More research on the aspects (e.g. micro-climate) of nest sites in flax compared to other habitats is needed. In the forest habitat, we might have observed shorter minimum inter-nest distances if there was a greater density of understory vegetation (i.e. not modified by introduced mammals such as deer, pigs, and cattle). However, it is unknown whether this would also lead to a greater number of nests at Hinahina Cove as this can be influenced by several other factors that were beyond the scope of our study.

In addition to adequate shelter from insolation, there are other factors that may affect the selection and distribution of hoiho nests. For example, topographical features such as slope can be important as hoiho require level ground at and within the immediate vicinity of a nest site (Seddon and Davis 1989). Anecdotal observations suggest that hoiho may defend a territory of up to 20 m around a nest site (Darby and Seddon 1990, Marchant and Higgins 1990). This could explain the average minimum inter-nest distances we observed in scrub and forest habitats. However, some inter-nest distances were less than 5 m in both studies, and displays of territorial aggression between neighbouring adults are rare (Seddon and Darby 1990). It has also been suggested that hoiho may rely on the visual and spatial cues of a nesting habitat, more than vocal cues, for the recognition of breeding partners or offspring, and also for a chick's recognition of its parents (Setiawan 2004). This suggests that hoiho may be attracted to nest sites with specific visual or spatial characteristics that help with the relocation of the nest, and the distribution of these familiar visual and/or spatial cues could therefore affect the distribution of hoiho nests. This may help explain the greater inter-nest distances observed in the forest habitat, where hoiho appeared to select sites comprised of distinguishable visual and spatial features (e.g. hollows under logs, large roots, and the base of tree stems) that also provided ample protection from insolation.

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In conclusion, our results provide support for the hypothesis that hoiho nest site selection and distribution appear to be influenced primarily by the location of structural micro-habitat features (e.g. a significant amount of cover particularly within 50 - 100 cm above the ground, and a solid backing) that provide optimal protection from insolation, and may help fulfil other potential requirements such as shelter from other climatic effects, and conspicuous visual/spatial cues that assist in relocation. Strong selection for these nest site features results in: 1) a high probability of visual concealment, 2) relatively large distances between nests (especially in habitats where suitable nest site features are available at lower densities), and subsequently 3) the typical but non-essential visual isolation of nest sites from conspecifics. The consequential visual concealment of nests may be beneficial for reducing the risk of predation and negative effects of disturbance from other animals and humans (e.g. nature tourism (Ellenberg *et al*. 2007)), but there is no concrete evidence that visual isolation from conspecifics is an essential requirement. The proximate cause of the nest failures attributed to a lack of visual isolation from conspecifics by Darby (1985) and Lalas (1985) may have been a detrimental frequency of disturbance. However, rather than visible exposure to neighbouring conspecifics, the ultimate cause of these failures may have been increased disturbance due to a lack of insolation cover (i.e. increased frequency of the incubating adult standing or leaving the nest for shade to relieve heat stress, thereby exposing the eggs to insolation). Furthermore, perhaps the nesting birds were inexperienced breeders, as was suggested for the reduced breeding success of some of the “open” nests in grazed grassland observed by McKay et al. (1999).

Nesting habitats comprised of relatively dense vegetation and/or other structures within 1 m of the ground may provide conditions that allow for greater nest densities than other habitats. However, as demonstrated in McKay et al. (1999) and reported in Marchant and Higgins (1990), where dense vegetation or other forms of cover are not available, hoiho can successfully nest in relatively open conditions where the nest backing structure and the aspect may provide enough shelter from insolation, though reduced breeding performance may be a consequence.

Recommendations

Future research should examine aspects of nest site micro-climate in more detail, and if possible, the potential relationships between the amount and/or type of nest site cover and the age or success of the breeding pair. We recommend that the restoration of hoiho nesting areas aim to produce structurally diverse nesting habitats with sub-canopy vegetation densities that vary at different heights (i.e. lower densities within 0 – 50 cm, and greater densities within 50 – 100 cm of the ground). This may eventually provide an optimal availability and quality of suitable nest sites, leading to greater nesting success and growth of the hoiho population within its South Island range. Lastly, we propose that authoritative texts and other sources of information on hoiho should be amended to reflect that the common visual isolation of nest sites from conspecifics is a consequence of selection for microhabitat features that provide, amongst other possible requirements, a significant amount of protection from insolation.

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Tables

Table 1. Sample sizes for: (1) the original data sets of active yellow-eyed penguin *Megadyptes antipodes* nests and randomly selected unused sites, (2) the data sets used in analyses of variables influencing nest site selection, and (3) the data set for the assessment of the mean minimum inter-nest distance, in flax and scrub habitats at Boulder Beach, and forest habitat at Hinahina Cove, New Zealand, 2006-2007.

Habitat and Site Type	Original	Variable Analyses	Mean Minimum Inter-nest Distance
Flax Habitat			
Active Nest	19	19	12
Random Unused	15	15	
Scrub Habitat			
Active Nest	12	11	8
Random Unused	15	12	
Forest Habitat			
Active Nest	14	12	12
Random Unused	12	10	

Table 2. Binary logistic regression models evaluated in an analysis of the relative importance of the mean maximum distance of visibility (V), and the mean % insolation cover (IC) in the selection of nest sites by the yellow-eyed penguin *Megadyptes antipodes*. Data for the models was collected at active nest sites and randomly selected unused sites in flax and scrub habitats at Boulder Beach, and forest habitat at Hinahina Cove, New Zealand, 2006-2007. Listed for each model are the Deviance (D = -2logLikelihood), number of parameters (K), the Akaike's Information Criterion value corrected for small sample sizes (AIC_c), the difference (Δ_i) between the AIC_c of each model and the lowest AIC_c, and the Akaike weight (w_i). The * symbol represents models that contained an interaction between V and IC, and the & symbol represents models that contained both V and IC.

Habitat	Model	K	AICc	Δ_i	w_i
Flax	IC	2	45.50	0.00	0.58
	V*IC	2	47.58	2.08	0.21
	V & IC	3	47.89	2.39	0.18
	V	2	51.00	5.50	0.04
Scrub	V*IC	2	19.09	0.00	0.72
	V & IC	3	21.62	2.53	0.20
	IC	2	23.53	4.44	0.08
	V	2	31.72	12.63	0.00
Forest	V & IC	3	14.48	0.00	0.49
	V	2	15.43	0.94	0.31
	V*IC	2	16.85	2.37	0.15
	IC	2	19.19	4.71	0.05

Figure Captions

Figure 1. Locations of the two yellow-eyed penguin *Megadyptes antipodes* nest site selection study areas, Boulder Beach and Hinahina Cove, on the southeast coast of the South Island of New Zealand, 2006-2007. The inset map indicates the region of New Zealand that is represented in the larger map.

Figure 2. Mean (±SE) maximum distance of visibility measured (to the nearest 0.5 m) at active yellow-eyed penguin *Megadyptes antipodes* nests (filled circles ●) and randomly sampled unused sites (hollow circles O) in flax and scrub habitats at Boulder Beach, and forest habitat at Hinahina Cove, New Zealand, 2006-2007. Sample sizes are provided in Table 1.

Figure 3. Mean (±SE) % insolation cover (derived from the mean diffuse non-interceptance) recorded at active yellow-eyed penguin *Megadyptes antipodes* nests (filled circles ●) and randomly sampled unused sites (hollow circles O) in (a) forest habitat at Hinahina Cove, and (b) flax and scrub habitats at Boulder Beach, New Zealand, 2006-2007. Sample sizes are provided in Table 1.

Figure 4. Scatter plots representing the relationship between mean maximum distance of visibility (measured to the nearest 0.5 m) and % insolation cover (derived from the mean diffuse non-interceptance) recorded at active yellow-eyed penguin *Megadyptes antipodes* nest sites in flax and scrub habitats at Boulder Beach, and forest habitat at Hinahina Cove, New Zealand, 2006-2007. The habitat type, Spearman's correlation coefficient (r_s) and associated significance (P) are indicated above each plot. The significant correlation in plot (c) is indicated in bold font. Sample sizes are provided in Table 1.

Figure 5. Scatter plots representing the relationships between mean minimum inter-nest distance (measured to the nearest 0.1 m) and the mean maximum distance of visibility (measured to the nearest 0.5 m), and mean % insolation cover (derived from the mean diffuse non-interceptance) recorded at active yellow-eyed penguin *Megadyptes antipodes* nest sites in flax and scrub habitats at Boulder Beach, and forest habitat at Hinahina Cove, New Zealand, 2006-2007. The habitat type, Spearman's

correlation coefficient (r_s) and associated significance (P) are indicated above each plot. The significant correlation in plot (b) is indicated in bold font. Sample sizes are provided in Table 1.

Figure 1

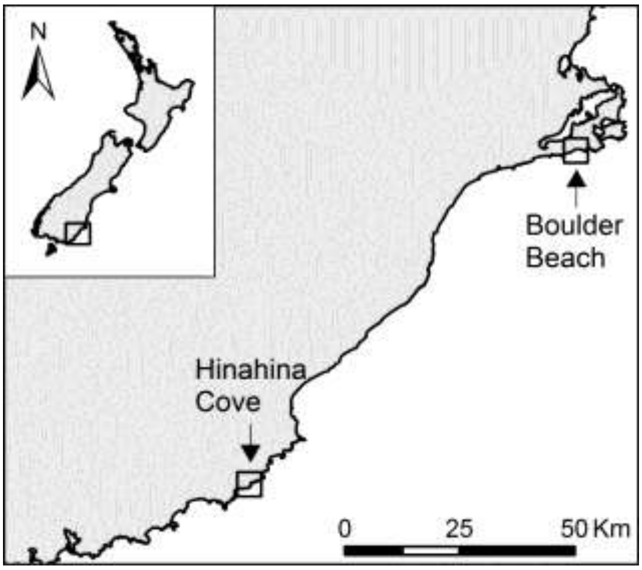


Figure 2

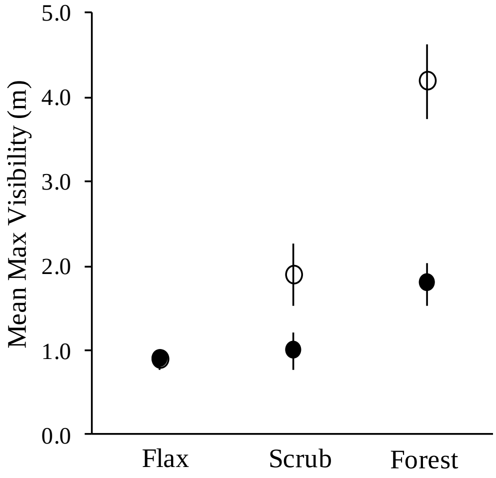


Figure 3

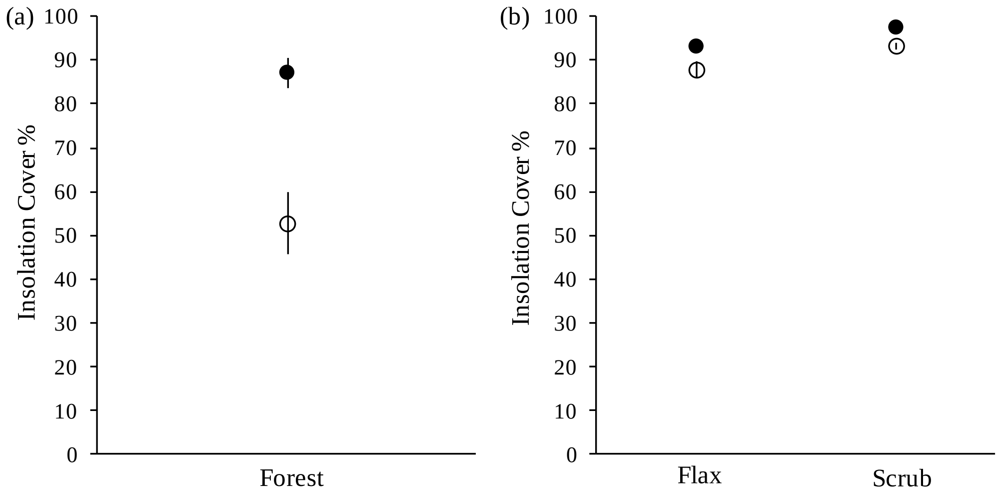
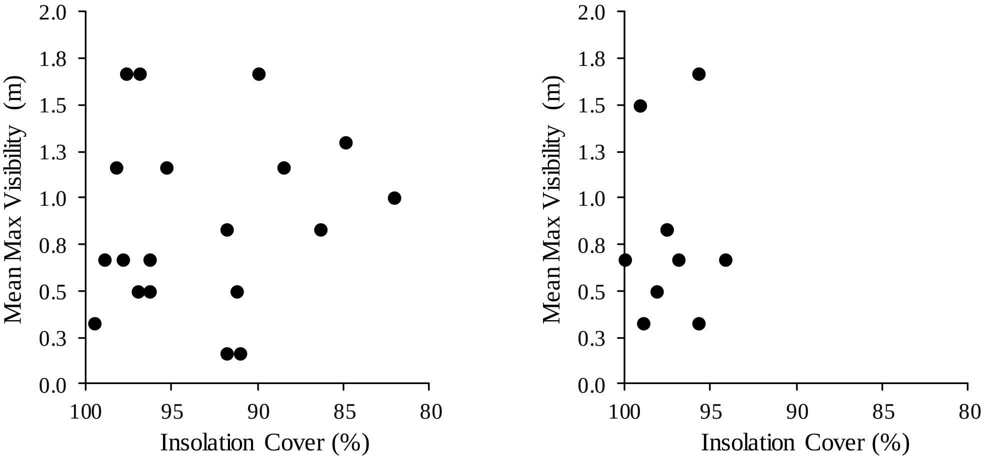

(a)
Insolation Cover %
100
90
80
70
60
50
40
30
20
10
0
Forest
(b)
Insolation Cover %
100
90
80
70
60
50
40
30
20
10
0
Flax
Scrub

Figure 4



(a) Flax (r_s = 0.18, P = 0.46)

(b) Scrub (r_s = -0.18, P = 0.6)

(c) Forest (r_s = 0.66, P = 0.02)

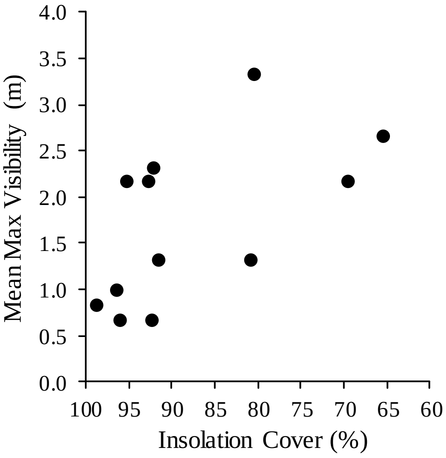
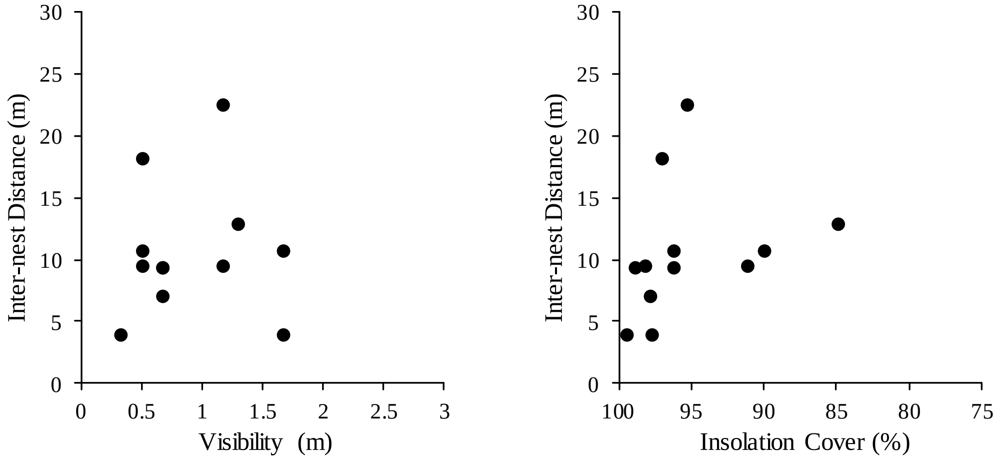
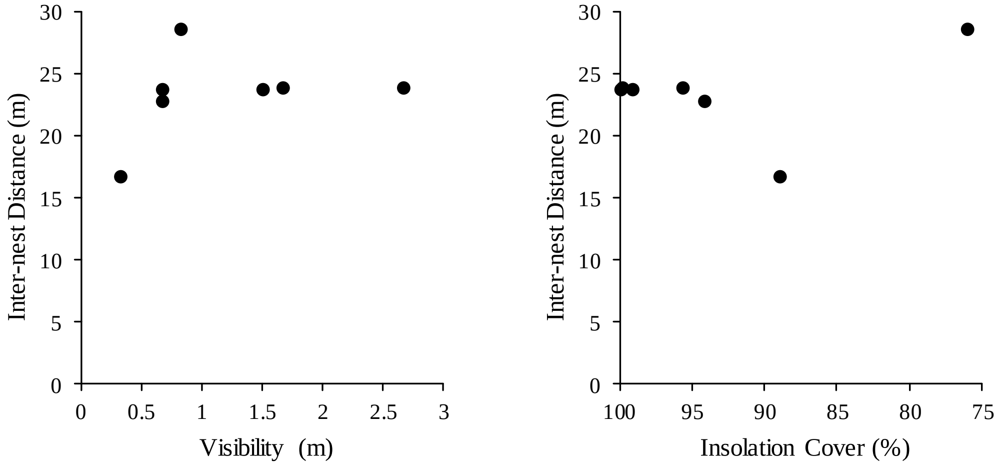


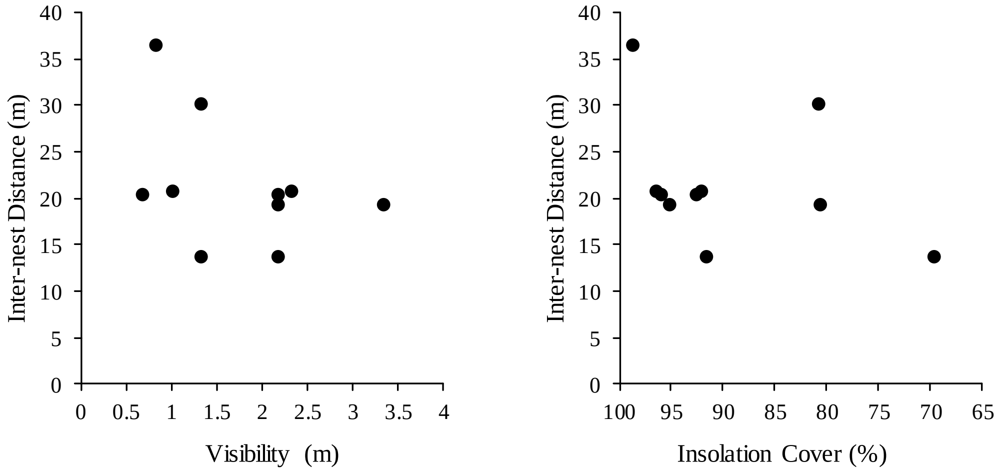
Figure 5


(a) Flax (r_s = 0.12, P = 0.71)

(b) Flax (r_s = 0.63, P = 0.03)


(c) Scrub (r_s = 0.63, P = 0.1)

(d) Scrub (r_s = -0.08, P = 0.85)


(e) Forest (r_s = -0.22, P = 0.48)

(f) Forest (r_s = -0.12, P = 0.71)