Assessing the impact of nest searches on breeding birds – a case study on Fiordland crested penguins (*Eudyptes pachyrhynchus*)

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Abstract: Long-term population monitoring has become an important tool for conservation management and indicator of environmental change. In many species nest counts are used as an index of population numbers. A pilot study using double-counts in Fiordland crested penguins (*Eudyptes pachyrhynchus*) found that up to 12% of nests had failed following the first count, raising concerns about search-related disturbance effects and the reliability of long-term monitoring data. Here, we assess the impact of nest counts, and provide recommendations on how to reduce human disturbance effects during nest searches. In 2011, miniature temperature loggers (iButtons) were deployed into 120 nests to quantify temporary and permanent nest abandonment. Observations at nest sites allowed subsequent analysis of a range of factors potentially affecting penguin disturbance responses. In almost a third of all nests both first and second searches caused temporary nest abandonment that lasted up to 4.5 h, creating considerable predation opportunities. To reduce the likelihood of nest abandonment, counts are best conducted during the second half of the incubation period when nests are attended by single, well-established adults. Steep nesting areas proved suboptimal for long-term monitoring. Actual nest failure rates were low in 2011 (about 2% per search) and not all failures were immediately related to search disturbance. Hence, double-counts may be used in Fiordland crested penguins to improve nest count reliability as long as predation pressure is low and field protocols are adapted to minimise disturbance impact of nest searches. We show that well-designed research projects can inform and improve management decisions. For gathering reliable long-term population data, we encourage the reassessment of best-practice protocols to minimise monitoring-related disturbance effects.

Keywords: double-counts; human disturbance; Lincoln–Peterson; New Zealand; population monitoring

Introduction

Long-term population monitoring is essential for effective conservation management (Thomas 1996; Şekercioğlu 2012) and an important tool for assessing environmental changes (Gregory & van Strien 2010). Nest counts are often used as an index of population numbers (Bibby et al. 1992). However, for cryptic breeding species that nest dispersed or in loose colonies, single nest counts will almost always yield an underestimate of true nest numbers (Walter & Rusch 1997) with no means to determine level of error. Double-counts, where the same area is searched successively by two independent teams with similar experience and effort, allow assessment of the number of nests missed during a single search and thus will provide a better estimate of actual nest numbers (Bart & Earnst 2002; Hegg et al. 2012).

Potential disturbance effects of long-term population monitoring are often neglected, although even a single nest count may have considerable impact on the breeding population. A pilot study using double-counts during 2010 found up to 12% of Fiordland penguin nests failed the following day, with cold abandoned eggs present in the nest bowls during second searches (JAH unpubl. 2010: Tawaki Monitoring – August 2010 Southern Islands Area. Internal Report DOCDM-657473, Department of Conservation, Invercargill). Thus concern has been raised that the better accuracy of double-counts may come at the cost of even higher nest failure rates than with single searches alone.

It is imperative to minimise the effects of nest-search-related disturbance, not only to minimise impact on breeding success, but also to gather accurate long-term monitoring data. Human disturbance is defined as any human activity that changes the contemporaneous behaviour and/or physiology of one or more individuals (Nisbet 2000). But identifying and quantifying disturbance-related effects can be challenging. Direct mortality (e.g. road kill, bycatch) may be immediately apparent; however, subtle and accumulating effects of human disturbance on susceptibility to disease, fertility, and life expectancy are currently not well understood. Human disturbance can alter hormonal stress response (Walker et al. 2005; Ellenberg et al. 2007) as well as energy budgets of adult birds (Ellenberg et al. 2013); reduce breeding success,

fledgling weights, and subsequent first-year survival (McClung et al. 2004; Ellenberg et al. 2006, 2007); and defer prospecting pairs from establishing a nest in disturbed habitats (Hockey & Hallinan 1981).

Stressful events may redirect an individual's behaviour towards survival rather than reproduction (Watanuki et al. 1993) consequently leading to temporary or even permanent nest abandonment (Wingfield et al. 1997). This creates predation opportunities and exposes the nest contents to the elements, which can affect embryo development. Short-term absence of an incubating parent is usually not much of a problem; however, dependent on predation pressure, breeding stage, and ambient climatic conditions, nest failure rates following human disturbance can be considerable (e.g. Hockey & Hallinan 1981). Once a nest fails, most penguin species do not re-lay and the reproductive output for the season is lost.

While some species appear to be relatively tolerant of humans, others such as Humboldt (*Spheniscus humboldti*) or yellow-eyed penguins (*Megadyptes antipodes*) are extremely sensitive to human disturbance (Ellenberg et al. 2006, 2007). Anecdotal evidence suggests Fiordland crested penguins (*Eudyptes pachyrhynchus*) are rather timid, although to date we have no scientific evidence of human disturbance effects.

Fiordland crested penguins arrive at their breeding colonies from mid-June onwards and the majority of nests are established by mid-July. Most pairs lay over a 10-day period around late July and early August (Mattern 2013a). Eggs are laid 3–6 days apart (St. Clair 1992). Once incubation is underway, pairs usually stay together at the nest sharing incubation duties for 5–10 days, until the female leaves for a 2-week foraging trip (unlike all other crested penguin species where the male leaves first; Warham 1975). Once the female returns, the male goes to sea for up to 2 weeks and usually comes back just before hatching (Mattern 2013a).

Since the likelihood of nest failure will depend on the time a nest is left unattended, nest attendance during and after human disturbance needs to be quantified. The use of iButtons, miniature temperature data loggers added into the nest, has been shown to be a practical method to remotely monitor animal attendance patterns while minimising human disturbance impact (e.g. Hartman & Oring 2006; Moore et al. 2010).

We assessed behavioural responses of incubating Fiordland crested penguins during nest counts and quantified actual nest failure rates. Based on our data we make recommendations on how to best reduce disturbance associated with nest searches. For reliable long-term population data we encourage the evaluation of monitoring protocols to minimise related disturbance effects.

Methods

Species and study sites

The Fiordland crested penguin (*Eudyptes pachyrhynchus*; Spheniscidae) is endemic to the south-west of New Zealand's South Island, Stewart Island, and outliers (Mattern 2013a; Ellenberg 2013). The IUCN Red List ranks the species as vulnerable (BirdLife International 2012). Within New Zealand, the Fiordland crested penguin is classified as threatened owing to low population size and suspected ongoing population decline (Miskelly et al. 2008).

Fiordland crested penguins breed in poorly delineated colonies and nests may be dispersed over considerable stretches of coastline (Mattern 2013a). The nesting habitat of these penguins is quite diverse, ranging from temperate rainforest or dense coastal shrubland, to sea caves and rock boulders. Most nests are located in hollows under fallen trees, roots, boulders or rock crevices. Ten breeding areas were searched during the incubation stage in late August 2011, covering most of the species' current range (Fig. 1, Table 1). The breeding areas selected for monitoring differ in predator exposure and monitoring history. While some sites were searched for the first time, others had been monitored for many years (up to 2010 via single nest counts). Monitoring areas were located on

Table 1. Breeding areas of Fiordland crested penguins (*Eudyptes pachyrhynchus*) searched in 2011 for active nests using double-counts. Search time of first (and second) searches is given in hours (hh:mm). Nest numbers ± variance were estimated using the Lincoln–Peterson model. The nest detection rates of the first and second search teams are provided.

Location	First search (dd:mm:year)	Search times (hh:mm)		Monitoring history	Predators	Nest numbers ± SD	Detection rate (%)	
		First	Second				First	Second
Jackson Head West[1,2]	15.08.2011	10:05	9:30	New 2010	Mainland[3]	74 ± 4.9	72	85
Stafford[2]	15.08.2011	8:00	7:30	New 2011	Mainland[3]	48 ± 0.0	83	100
Shelter Islands 3	16.08.2011	1:25	1:35	Since 1994	Weka[4]	17 ± 0.1	94	94
Shelter Islands 4	16.08.2011	2:10	1:36	Since 1994	Weka[4]	17 ± 2.0	71	76
Breaksea Island, hut	17.08.2011	1:59	1:45	Since 1996	Free[5]	24 ± 0.1	92	95
Breaksea Island, 60 m	17.08.2011	2:40	1:36	Since 1996	Free[5]	34 ± 4.2	79	67
Martins Bay[1], 1	23.08.2011	1:35	0:50	Since 1994	Mainland[3]	14 ± 0.0	100	86
Martins Bay[1], 2	23.08.2011	1:56	1:30	Since 1994	Mainland[3]	26 ± 0.1	92	92
Codfish Is, Mephistopheles	29.08.2011	7:42	6:35	Since 1997	Free[6]	80 ± 4.3	90	90
Codfish Is, North Head	29.08.2011	5:45	3:41	New 2010	Free[6]	40 ± 3.4	73	93

[1]Easily accessed by tourists and hunters; stoats, rats, and possums present, no ferrets, occasional (illegal) dogs.
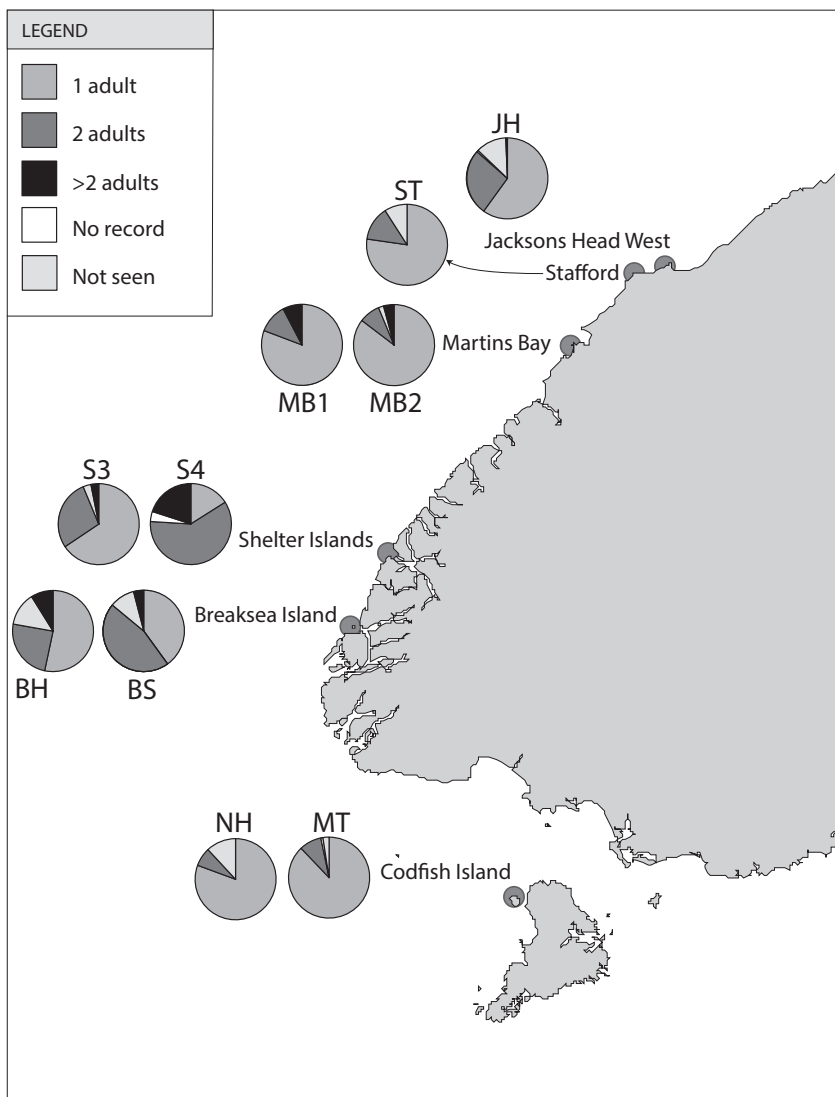[2]Clearly defined subsection of larger breeding area is monitored.
[3]'Mainland' breeding areas are exposed to the usual suite of predators, most importantly stoats.
[4]Weka is a New Zealand endemic rail that may opportunistically prey on penguin eggs.
[5]Rats eradicated 1988.
[6]Possums eradicated 1984–1987, weka eradicated 1980–1985, kiore eradicated 1998.

Figure 1. Map of the New Zealand South Island and Stewart Island showing all breeding areas of Fiordland crested penguins (*Eudyptes pachyrhynchus*) included in this study. Most abbreviations of monitoring areas are self-explanatory: on Codfish Island MT stands for 'Mephistopheles' and NH for 'North Head'; on Breaksea BH is by the hut and BS is 60 m away. The numbers of adults encountered at the nest during first searches in each breeding area are shown in the legend. Note the difference in nest attendance on Breaksea and the Shelter Islands compared with all other breeding areas.

predator-free offshore islands, islands with weka (*Gallirallus australis*, an endemic rail known to opportunistically prey on penguin eggs), and on the mainland, where the penguins are exposed to a suite of introduced predators most importantly stoats (*Mustela erminea;* Table 1). None of the studied mainland breeding sites currently receives any predator control.

iButton deployment

The iButton® (DS1922L-F5#, Maxim Integrated, San Jose, CA, USA) is a temperature data logger enclosed in a 'button-shaped' 17.5 × 6 mm stainless steel capsule that withstands harsh environments. Each iButton has a unique ID integrated in its circuitry. The devices record ambient temperature with an accuracy of ±0.5°C (from −10°C to +65°C). Data are stored in an internal memory (8192 bytes of 8-bit units). In 2011, iButtons were programmed to record temperature at 30-s intervals which yielded temperature data for c. 68 h, thus covered the entire nest search period.

Non-toxic green spray paint was used as camouflage to make the devices less conspicuous. To reduce losses of iButtons, the devices were fixed to either a 9-cm flathead nail (to fix the iButton in nests on soft ground) or a 55-mm washer (to be placed in nests on rocky surfaces) using Knead-IT® STEEL (Selleys steel polymer repair system). Immediately prior to deployment the iButton was warmed up in the hand to create a spike temperature reading to facilitate determination of iButton placement time from the recorded data.

iButtons were deployed by the first search team at all sites except Breaksea and Shelter Islands where iButton retrieval would have been logistically too challenging. A total of 120 iButtons were deployed in all temporarily abandoned nests, and alternating to half of the attended nests, to evaluate potential disturbance created by iButton deployment in addition to the standard nest searches. Deployments involved a slow approach by one observer who carefully placed the iButton into the nest bowl by slipping a hand under the penguins' body if it continued to stay on the clutch (http://vimeo.com/80895273). The total deployment process never took more than one minute. The GPS position of the nest was determined simultaneously to minimise time spent in proximity of a nest. To facilitate the interpretation of iButton data in relation to behaviour, 11 nests were equipped with generic weatherproof surveillance cameras. At least one reference station was established in each monitoring area near the deployed nests and in similar habitat. Further reference stations were placed in rock cave sub-colonies to account for differences in microclimate.

At the end of each breeding season when birds had left their colonies for pre-moult foraging trips, iButtons were

recovered using a metal detector (Gold Bug 2, Fisher Labs, Texas, USA). Following the breeding season, some iButtons were found buried in up to 10 cm of solid nest contents and up to 4 m downhill from the nests if unanchored. On a few occasions we found two iButtons together in one nest indicating attractiveness for nest ornamentation. Upon retrieval it was noted if the iButton was found within the nest bowl or outside (metres away). iButtons buried deeply in solid nesting material at the end of the breeding season were interpreted as indicative of successful chick-rearing.

Double-counts

In each monitoring area, active nests were counted by two independent teams to estimate actual nest numbers and to assess nest-count reliability (i.e. proportion of nests missed during single searches). Mark–resight data allow estimation of the total number of nests, N, via the Lincoln–Peterson model:

$$N = \frac{(n_1 + 1) \times (n_2 + 1)}{m + 1} - 1$$

with n_1, number of nests found by the first team; n_2, number of nests found by the second team; and m, number of nests marked by the first and found by the second team. This approach requires that (1) sightings of first and second teams are independent; (2) detection probabilities are similar for all nests; (3) nests are clearly identifiable; (4) the population is closed, i.e. nests do not get newly established or lost entirely between the two searches (Williams et al. 2002). The nest detection rate (Table 1) was calculated by dividing the number of nests found by each team (n_1, n_2) by the estimated total number of nests (N).

First and second searches were alternated between teams. Areas were searched on consecutive days. No results were exchanged between the teams, to maximise independence of counts. All sites were searched by matched teams of two persons with one experienced leader. Each team carried at least one hand-held global positioning unit (GPS; model GPSMAP 60CSx; Garmin International, Olathe, KS) to track their movements and to record the location of any nests found. Searches ended when team members were satisfied the area had been covered thoroughly. If nest searches had to be stopped prematurely due to nightfall or inclement weather, the exact area covered was communicated to the second team by means of a topographic map.

A nest was defined as a formed bowl with one or more eggs, regardless of the presence of a bird at the time when it was found. Unattended eggs were checked if still warm (presumably abandoned due to search activity) or cold. Birds encountered sitting tightly on a well-established nest bowl were assumed to be incubating even if nest contents could not be established. Individuals or pair of birds attending a suitable but empty nest bowl were noted but not recorded as a nest.

Each nest found by the first team was marked with a small blue plastic triangle (90 mm, containing random number and year) at about 0.5–1 m distance from the nest bowl and just out of reach of the bird. Additionally, the first team marked the nest with a small spray colour spot (green for nests deployed with iButtons, purple for other nests) next to the marker in case the marker was lost. Care was taken that the marker and spray spot were placed in a way that it did not guide the second searchers to the nest. The second team removed all markers as a control and marked the iButton nest clearly with flagging tape to facilitate recovery of devices at the end the season. The following information was recorded at each nest: nest ID, new or resighted, GPS fix accuracy, iButton ID (if deployed), nest status (number of eggs), number and presence/absence of adult(s), habitat, presence of nest-back, lateral concealment, and slope (see Table 2). In cases where the adult fled, we noted flight initiation distance (FID – the distance between the observer and the nest at which the bird took flight) and the maximum distance the bird moved away from its clutch (DF) or if the bird fled out of sight.

Table 2. Definition of factors and levels (including coding of factor levels in R). Listed factors were considered for plausible a priori-defined candidate models to analyse what affected the likelihood of temporary nest abandonment during searches for nests of Fiordland crested penguins (Eupdyptes pachyrhynchus).

Factor	Definition
Location	Penguin breeding area monitored (10 distinct locations covering entire breeding range; see Table 1, Fig. 1)
Date	Searches were conducted over a period of 2 weeks during the incubation stage, thus the potential effect of date was expected to follow a linear relationship
History	Breeding areas have been monitored either recently added to the monitoring scheme 'new' (1) or regularly over many years in the past 'regular' (2) (Table 1)
Predators	Breeding areas differed in their predator presence i.e. predator 'free' (1), 'weka' present (2), or were exposed to a 'mainland' (3) suite of predators (Table 1)
Adults	Number of adults attending the nest, i.e. single (1) or pair (2)
Habitat	Nesting habitat was characterised into the following: dense 'kiekie' *Freycinetia banksii* scrub, 'rock', 'rock cave', coastal 'shrub', 'tree cave' usually situated under huge fallen trees, 'tree root', 'other' included tall grass, grassy and rock ledges
Cave	'Cave' (1) – irrespective of material (earth, rock or wood) – or 'not' (2)
Nest-back	'Back' (2) means nest is situated against a solid rock, earth or plant wall, or 'not' (1)
Lateral cover	Amount of vegetation or other sight obstruction at penguins' eye-level i.e. 0-1m above ground: '<50%', '50-75%' and '75-100%'
Slope	Gradient of habitat around the nest site: 'flat' (1), 'moderate' (2), 'steep' (3) – the latter required observer to use hands to move around
Steep	Considering only two slope levels: 'moderate/flat' (1) and 'steep' (2)

Statistical analysis

For the analysis of factors potentially affecting the probability of nest abandonment a binary logistic regression model was run in R version 2.15.2 (R Development Core Team 2008). The response variable was coded as '1' (adult present on nest) or '0' (incubating bird fled). All factors listed in Table 2 were included into plausible a priori-defined candidate models. Models were ranked using Akaike Information Criterion (AIC) as the relative goodness of fit for each model (Anderson 2008).

In order to quantify penguin disturbance responses a range of classical statistical tests were employed. Linear regression was used for testing potential effects of cumulative time spent in the proximity of a nest and frequency of disturbance (determined from GPS track logs) on the likelihood of nest abandonment. A paired t-test was used to compare behavioural responses (e.g. FID, DF) during first and second searches to assess habituation potential. Pearson's chi-square test was used to determine whether the behavioural responses to human approach were correlated during first and second searches. To assess stress-coping styles, a two-tailed t-test compared independent means of responses, such as the time a nest was unattended with birds staying close to the nest compared with those of birds fleeing greater distances. Homogeneity of variances was tested using Levene's test and data transformed if required. For traditional statistical approaches differences were considered significant if $P < 0.05$. We report values as mean ± SD if not indicated otherwise. Birds that had returned from their initial flight were prone to flee again when searchers returned past the nest due to habitat restrictions. Therefore, if a clutch was left unattended several times during one search day, the first temporary nest abandonment caused by human proximity was used for statistical analysis to avoid pseudo-replication.

Results

During first searches of Fiordland crested penguin breeding areas monitored by DOC in 2011 we found 290 nests. Of these, 257 nests were resighted during second searches. Using the Lincoln–Peterson model we estimated a total of 375 ± 14 active nests were actually present in the searched areas, with estimated numbers at each monitoring site varying between 14 and 80 ± 4 nests (Table 1).

Potential impact of iButton placement

Placing an iButton into the nest bowl usually did not affect the behaviour displayed by the attending adult (http://vimeo.com/80895273). In six nests (5%) iButton placement caused temporary abandonment of a previously attending adult. Of the nine nests found permanently abandoned during second searches, three had been equipped with an iButton the day before.

## Timing of searches during the breeding cycle

The status of 76 nests could be confirmed during both first and second searches. Of 17 one-egg clutches observed during first searches, four contained two eggs during the second search. Hence, at least 5% of the breeding pairs had not yet completed their clutch when nest searches took place in 2011. In 175 nests the number of attending adults was observed and recorded during both visits. The number of adults at the nest was significantly related between first and second visits (Pearson's chi square: $\chi_{175} = 18.2$; $P < 0.001$) with 121 (69%) of nests being attended by a single adult during both visits. The remaining 31% of nests had two adults attending during at least one of the visits. Date had a significant effect on the likelihood of encountering both parents at the nest. Single adults were more likely observed during searches that took place later in the season ($t_{146} = 5.17$, $P < 0.001$; Fig. 2).

Fiordland crested penguins were not synchronised in their onset of breeding. Judging from the number of nests that were still attended by pairs during nest searches the onset of breeding may vary even between neighbouring colonies. Most strikingly, penguins at Breaksea and the Shelter Islands in central Fiordland appear to commence breeding considerably later than at all other sites (Fig. 1). Thus the numbers of loafers (i.e. non- or not-yet breeding birds that are not attached to a nest and thus more prone to flee) was comparably higher in central Fiordland colonies.

Nest failures following first searches

On the West Coast, five previously active nests (2% of resighted nests) definitely failed. During second searches we found two unattended and cold clutches and three empty nests, one of which was attended by a tightly sitting adult.

In predator-free Fiordland monitoring areas, another four (1.6%) marked nests were found empty and unattended during second searches; however, none of these was confirmed as
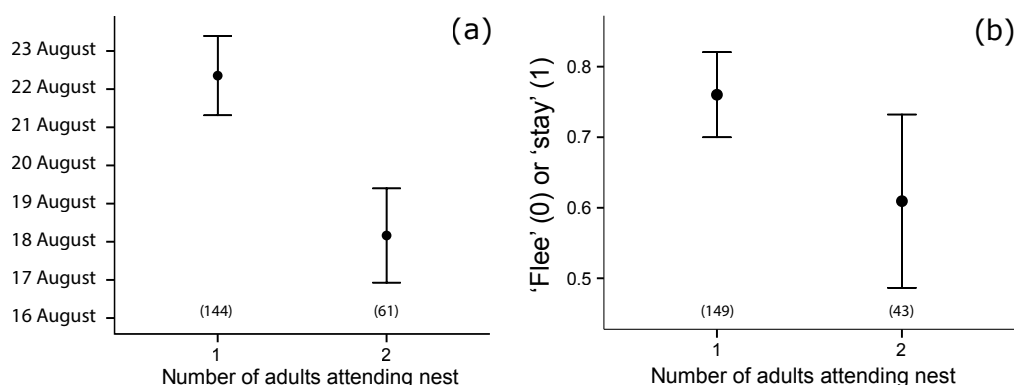
Figure 2. Number of Fiordland crested penguin (*Eudyptes pachyrhynchus*) adults attending their nest in relation to (a) date of first searches and (b) observed behaviour when marking the nest, i.e. staying on the nest (1) or taking flight (0). Number of cases (*n*) is given in brackets. Only cases where the nest was clearly attended by either one or two adults were considered. Error bars depict 95% confidence intervals.

active (i.e. containing eggs) the previous day. Hence, these nests were likely yet to be established.

On Codfish Island, one failed, unmarked nest containing one cold egg was found during the second search within a sub-colony in coastal shrub and only a few metres away from a marked nest. However, since this nest had not been observed by the first team it is unclear whether failure was caused by human disturbance or if the nest had failed earlier.

Interpreting iButton data

A total of 82 iButtons could be recovered. Of these, 73 yielded good data including 10 iButtons from reference stations, 6 from nests equipped with surveillance cameras, and 57 iButtons that had been placed into nests exposed to double-counts: Jackson Head (15), Stafford (15), Martins Bay (10), Mephistopheles (8), and North Head (9). The remaining nine iButtons had corrupted data.

The iButton data clearly showed if a nest continued to be active following search disturbance (e.g. Fig. 3a). Although a nest may have been temporarily abandoned during human approach the birds usually came back and resumed incubation. In other cases iButton data confirmed failure following disturbance. For instance, upon return one bird never settled back properly to resume incubation (Fig. 3b). This nest was permanently abandoned c. 2 h after iButton placement and found empty the next day. In some cases the birds stayed on their clutch during the first approach but responded more strongly during subsequent disturbances when neighbouring nests were recorded (Fig. 3c). Camera footage greatly aided in interpretation of iButton data. Temporary absence from the clutch, e.g. during partner changeover or fight with trespassing conspecifics, resulted in temperature declines similar to those observed during nest desertion caused by human disturbance. However, natural absences observed via surveillance cameras were considerably shorter, generally lasting a few minutes only.

Of the 57 nests for which we have temperature data, six nests appear to have failed in the course of nest searches (three between first and second count, and one to three may have failed following the second visit). Between three and five nest failures may be attributed to human disturbance. In two cases the eggs disappeared between searches. The third nest (a well-incubated two-egg clutch) was abandoned due to second searches for 13:49 h. Prior to the onset of incubation fertile eggs can stay alive for several days. Once incubation has commenced penguins usually do not leave their eggs for more than a few minutes, e.g. during social interaction. Depending on ambient climatic conditions unattended eggs may survive for a few hours and still hatch (anecdotal evidence in yellow-eyed penguins, author's pers. obs.). However, in this case prolonged absence of the incubating bird will have likely caused breeding failure, with average temperatures of 9°C measured in the nest bowl during the time the nest was left unattended.

One nest was permanently abandoned (eggs found cold the next day) almost 8 h after the iButton was placed during which observers caused only temporary nest abandonment (for 8 min), thus this nest likely failed due to natural causes. Two failures were inconclusive due to lack of data. As field protocols focused on flighty birds (with iButtons deployed in every second attended nest only; see Methods), adjusted numbers suggest a total of 3–5% of all nests may have failed due to first (2%) and second nest searches (1–3%).

Likelihood to flee from searchers

About one-third (31.9%) of all incubating birds (n = 290) fled when searchers approached during first searches. Half of these individuals (52%) remained in the proximity of the nest (< 3 m) and usually settled back into the nest bowl shortly after the person retreated, while the other half (48%) fled considerable distances and often out of sight. iButton data confirmed that birds that stayed close to the nest needed significantly less time to resume incubation than birds that fled further or out of sight (time, ln-transformed for equal variances: t_{12} = −3.93; P = 0.002).

The relative frequency of previously incubating birds observed fleeing differed considerably among the 10 monitoring sites (Fig. 4). To better understand what factors contributed to the birds' decision to flee or stay on the nest, we conducted a binary logistic regression analysis to predict the likelihood of temporary abandonment for 290 clutches found during first searches. Of the candidate models considering all plausible factors, the following model was ranked highest when models were compared using Akaike's Information Criterion as the relative goodness of fit (Table 3).

The probability (P) that the attending adult does not abandon the nest was

$$P = \frac{1}{1 + e^{-z}} ,$$

where $z = -0.62x_1 - 1.34x_2 + 2.08$, with x_1 = number of adults attending the nest, and x_2 = slope at the nest site (factor "steep", for coding of factor levels refer to Table 2). The likelihood of taking flight depended on:

1. The number of adults at the nest and thus timing of nest searches during the breeding cycle. Single adults were less likely to flee than birds on nests attended by two adults (presumably earlier incubation stage; Fig. 2).

2. The slope at the nest site. Birds nesting in flat or moderate situations were less likely to flee than birds nesting in steep habitat (Fig. 5a).

Since flight frequencies in 'flat' and 'moderate' terrain were similar, the factor 'steep' grouping these two into one category was a better predictor than 'slope' (model 6). Model probabilities (AIC weights; Table 3) show that the first five models have 10% or more chance of being the best model in this comparison and, thus, contribute considerably to understanding why birds fled. All five models include the above-stated two most important parameters: number of adults and steepness of terrain. Additionally, factors affecting the visibility of the searchers or escape routes for the birds such as lateral concealment (model 2) and presence of a nest-back (model 4) appear to play an important role for predicting the likelihood of taking flight. A bird was more likely to stay with increasing lateral concealment of the nest (Fig. 5b) and if situated against a nest-back. In comparison habitat (model 9) played a less important role. Furthermore, factors that relate to the onset of breeding, i.e. number of adults encountered at the nest, appear important ('date', model 3; 'location', model 5).

## Effect of nesting habitat on penguin disturbance responses

We found 89% of 366 nests backing on to a structure of some kind (nest-back). In 2011 nests were established in tree caves (22.3%), rock caves (17.1%), under boulders (5.4%), among tree roots (7.8%), in dense kiekie (21%), coastal shrub (18.4%), and other (7.3%). The category 'other' included grass, grassy
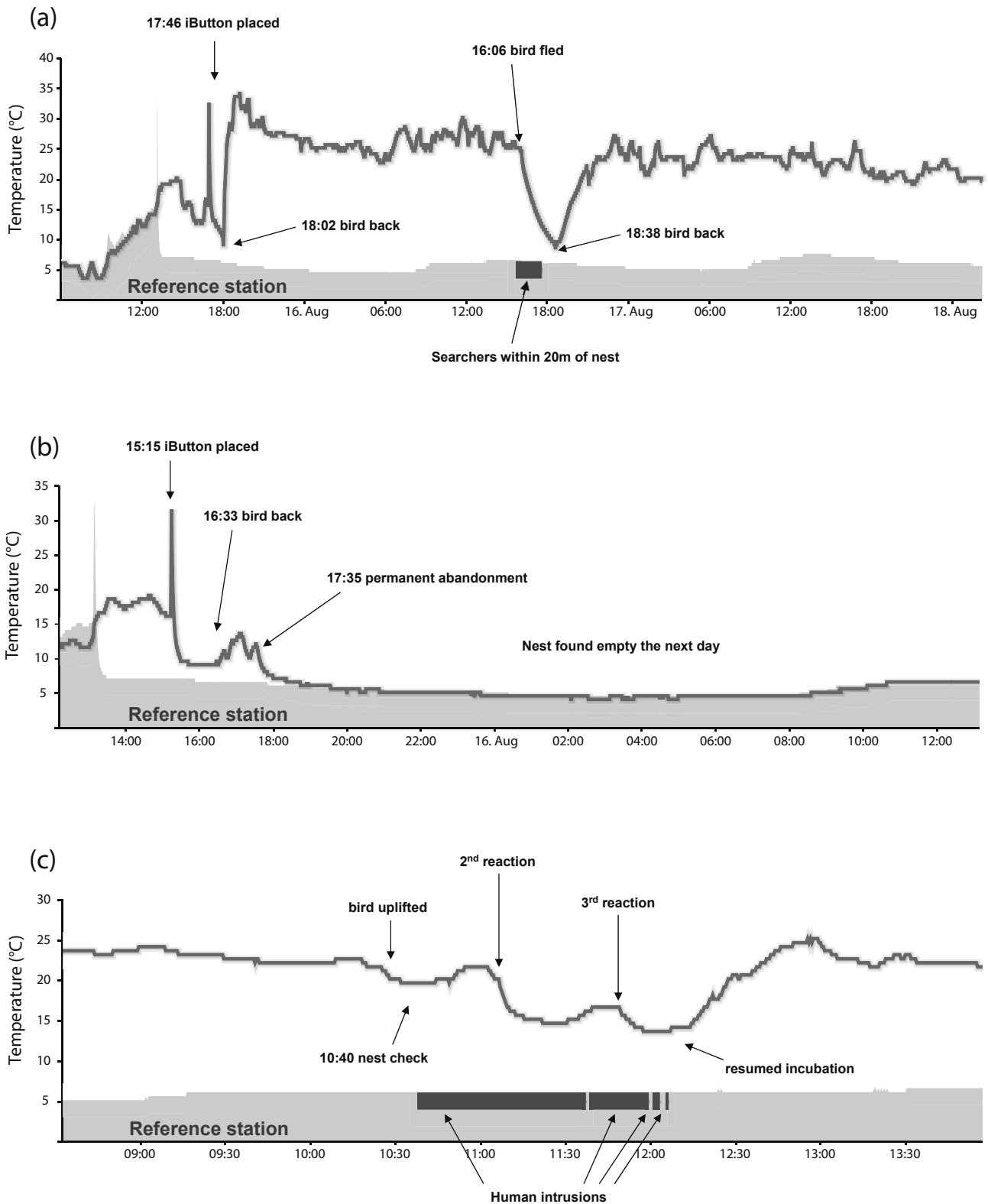
Figure 3. Example of iButton temperature reading over time (a) in a successful nest attended by a flighty individual and (b) in a nest that failed following first searches. (c) Detail of iButton temperature reading over time depicting three responses that caused nest temperature reduction during human proximity (solid bars) – the bird did not leave during the check but moved off the nest when the observer had to pass again later due to habitat constraints. Dark line depicts the temperature curve in degrees Celsius recorded in the nest, the light grey area in the background shows the temperature curve recorded by the corresponding reference station, and the dark bar indicates human presence within 20-m distance from the nest during second searches. Temperature spikes show the time when each iButton was deployed in the field. Inserted text describes the temperature curve in more detail for easier interpretation.
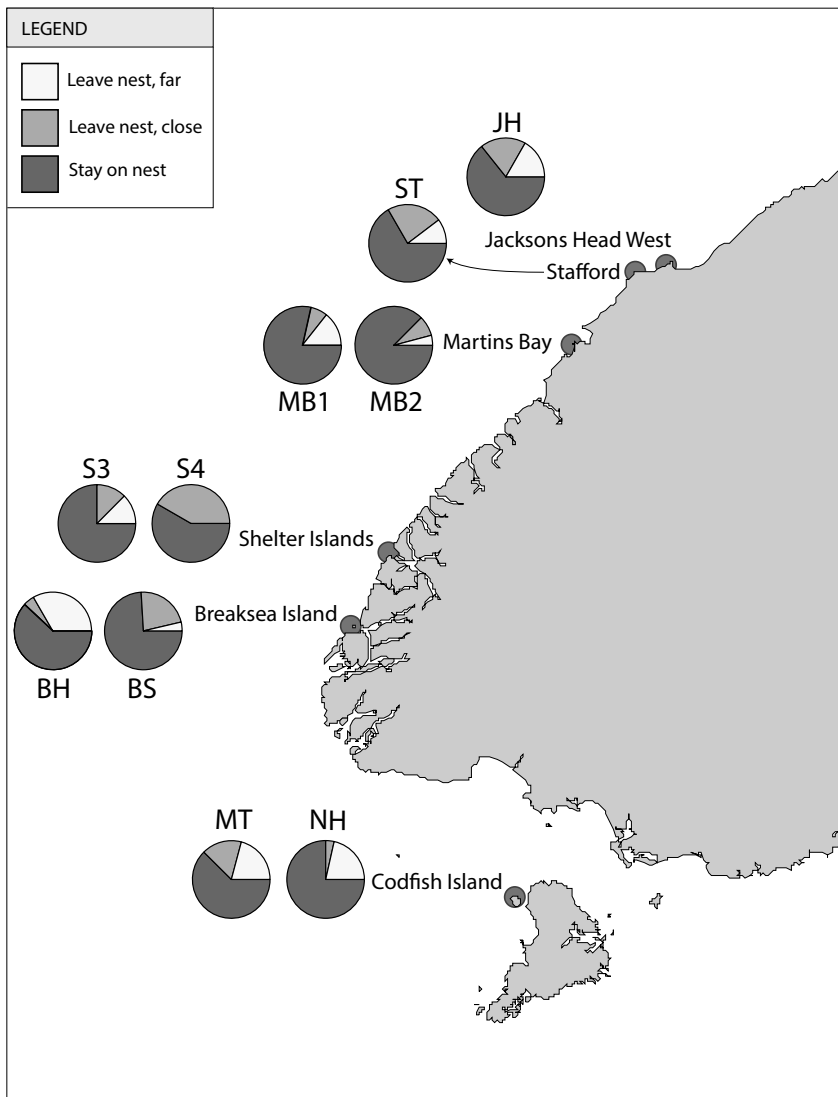
Figure 4. Map of the New Zealand South Island and Stewart Island showing all breeding areas of Fiordland crested penguins (*Eudyptes pachyrhynchus*) included in this study. Most abbreviations of monitoring areas are self-explanatory: on Codfish Island MT stands for 'Mephistopheles' and NH for 'North Head'; on Breaksea BH is by the hut and BS is 60 m away. The frequency of behavioural responses of incubating penguins to approaching searchers for each breeding area was categorised as either: 'stay'; 'close', i.e. temporary nest abandonment but remaining within 3 m of the nest bowl; or 'gone far', i.e. fleeing further and often out of sight.
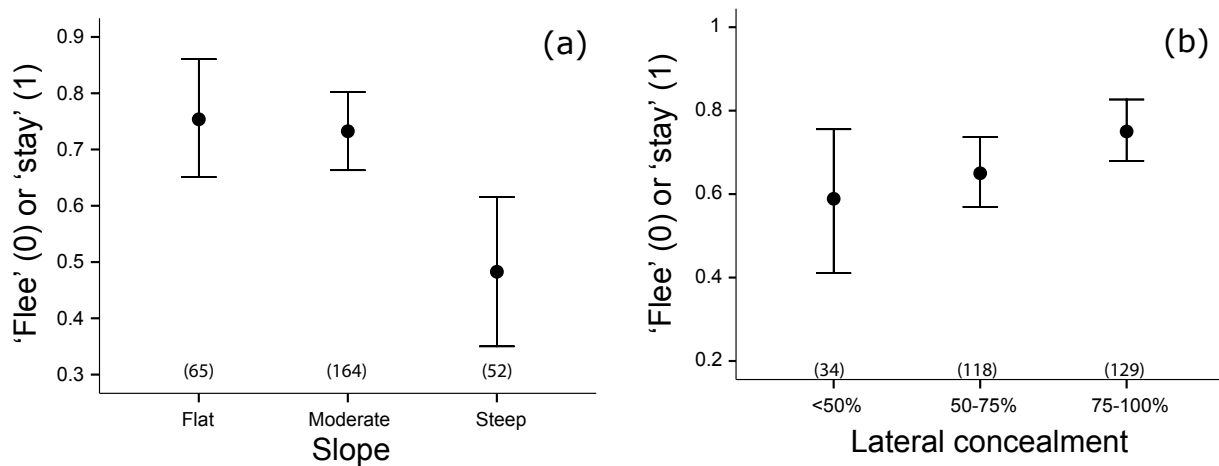
Figure 5. Behaviour (i.e. stay on (1) or abandon (0) nest) of Fiordland crested penguin (*Eudyptes pachyrhynchus*) adults depended on (a) slope at nest site, i.e. flat, moderate, and steep, with the latter describing situations where observers needed their hands to move around, and (b) lateral concealment of the nest measured in percent of lateral cover from ground level to 1 m high. Error bars depict 95% confidence intervals.

Table 3. Probability of nest abandonment in Fiordland crested penguins (*Eudyptes pachyrhynchus*) during first searches as a function of adult attendance, date, and site characteristics. Binary logistic regression models were ranked considering Akaike Information Criterion (AIC) as the relative goodness of fit.

Ranking	Candidate models	AIC	BIC	Deviance	ΔAIC	Model likelihood	AIC weight
1	P ~ adults + steep	290.73	301.42	284.73	0.00	1.00	0.25
2	P ~ adults + steep + lateralcover	291.61	305.85	283.61	0.88	0.64	0.16
3	P ~ adults + steep + date	291.89	306.13	283.89	1.16	0.56	0.14
4	P ~ adults + steep + nest-back	292.49	306.73	284.49	1.76	0.42	0.11
5	P ~ adults + steep + (1 | site)	292.62	306.86	284.62	1.89	0.39	0.10
6	P ~ adults + slope	292.68	306.92	284.68	1.95	0.38	0.10
7	P ~ adults + steep + history	292.71	306.95	284.71	1.98	0.37	0.09
8	P ~ adults + steep + predators	294.38	312.18	284.38	3.65	0.16	0.04
9	P ~ adults + steep + habitat	298.05	330.10	280.05	7.32	0.03	0.01
10	P ~ adults	304.99	312.11	300.99	14.26	0.00	0.00
11	P ~ adults + lateralcover	305.24	315.92	299.24	14.51	0.00	0.00
12	P ~ adults + (1 | site)	306.21	316.89	300.21	15.48	0.00	0.00
13	P ~ adults + history	306.81	317.49	300.81	16.08	0.00	0.00
14	P ~ adults + date	306.85	317.53	300.85	16.12	0.00	0.00
15	P ~ adults + nest-back	306.99	317.67	300.99	16.26	0.00	0.00
16	P ~ adults + predators	308.95	323.20	300.95	18.22	0.00	0.00
17	P ~ steep + lateralcover	346.76	357.73	340.76	56.03	0.00	0.00
18	P ~ steep + nest-back	348.39	359.36	342.39	57.66	0.00	0.00
19	P ~ steep	349.28	356.59	345.28	58.55	0.00	0.00
20	P ~ steep + (1 | site)	350.93	361.90	344.93	60.20	0.00	0.00
21	P ~ lateralcover	356.69	364.00	352.69	65.96	0.00	0.00
22	P ~ history	359.01	366.32	355.01	68.28	0.00	0.00
23	P ~ 1	359.78	363.44	357.78	69.05	0.00	0.00
24	P ~ nest-back	360.21	367.52	356.21	69.48	0.00	0.00
25	P ~ date	360.29	367.60	356.29	69.56	0.00	0.00
26	P ~ habitat	362.92	388.51	348.92	72.19	0.00	0.00
27	P ~ predators	363.53	374.50	357.53	72.80	0.00	0.00

The factor 'steep' considers only two levels, either flat–moderate or steep.
BIC = Bayesian Information Criterion; model likelihood = EXP(ΔAIC/2); model probability = model likelihood / sum of all model likelihoods in this comparison.

ledges, rock ledges, etc. and was the only category that had a significant effect on probability of taking flight. When pooling habitat categories further into 'cave', 'shrub', and 'other' again only birds attending 'other' nests were more likely to flee. Frequency of flight responses for penguins nesting in all remaining habitat categories was similar.

Flight responses comparing first and second searches

Similar to first searches, about one-third (31.4%) of all incubating birds abandoned their nest when being approached during second searches. Hence the likelihood to observe a flight response remained the same during both searches (paired *t*-test: $t_{193} = 0$, $P = 1$). The individual decision to stay or flee was highly correlated between first and second searches (Pearson's chi square: $\chi_{194} = 69.93$; $P < 0.001$) with the majority of individuals (114; 58.8%) staying on the nest during both visits.

The distances the birds fled (DF) were significantly reduced during second searches (from on average 12 m to 5.5 m), while the flight initiation distance (FID) remained the same during both searches (Table 4). Although birds remained unmarked to reduce disturbance impact, judging from nest attendance pattern observed by Warham (1975) it is likely that once a nest is attended by a single adult chances are high to encounter the same adult on the nest during consecutive days.

There was no significant difference in any of the disturbance response parameters (FID, DF, time absent, etc.) measured between nests attended by one or two adults. However, consistent with the overall model, if both partners attended an iButton nest they were more likely to flee.

Of the 57 iButton nests, 29 birds (51%) fled during first searches; another two (3.5%) likely fled after the searchers had left. However, 13 birds that previously fled stayed during the second visit, whereas six that stayed during the first visit fled during the second. Only 14 iButton birds were observed fleeing during both visits. These birds resumed incubation <1 h following first searches, but were on average >3 h absent from their clutch following second searches (Table 4).

The time a nest was left unattended due to first searches ranged from 0:04 to 5:41 hours; whereas during second searches nests were abandoned for 0:13 to 13:49 hours. When excluding the nests that are thought to have failed, significances remain similar to what has been presented in Table 4. However, ranges become smaller with 0:04 – 3:05 hours' absence due to first searches and 0:13 – 4:41 hours' absence due to second searches.

Overall, it appears that birds were less flighty during second searches. Of nests with iButtons that remained viable, 50% of the birds fled during the first search, whereas only 37% fled during the second search. However, responses remain correlated (Pearson's chi square: $\chi_{54} = 6.2$, $P = 0.013$). Of 15 clutches that were found unattended but warm during first searches, 11 had an adult attending during the second search, although five of these still fled when being approached.

Table 4. Differences in human disturbance events and disturbance responses of Fiordland crested penguins (*Eudyptes pachyrhynchus*) between first and second searches in 2011. Cumulative intrusion time (i.e. time observers spent within 20 m of the nest as derived from GPS track data) and the frequency of disturbance (numbers of intrusions into the 20-m perimeter of the nest) quantify the intensity of human disturbance. Penguin disturbance response is measured according to the flight initiation distance (FID), the distance the bird fled (DF), and the time the bird needed to return to the nest and resume incubation (derived from iButton data).

	First search mean ± SD (*n*)	Second search mean ± SD (*n*)	Paired *t*-test (d.f.)	*P*-value
Cumulative intrusion time (h:mm)	2:16 ± 0:57 (17)	1:20 ± 0:28 (17)	5.38 (16)	<0.001
Number of intrusions (*N*)	6.9 ± 5.1 (17)	3.8 ± 2.1 (17)	2.64 (16)	0.018
Flight initiation distance (m)	2.3 ± 1.3 (27)	1.9 ± 1.6 (27)	0.86 (26)	0.398
Distance fled (m)	12.3 ± 9.3 (24)	5.5 ± 6.4 (24)	3.75 (23)	0.001
Time absent from nest (h:mm)[1]	0:46 ± 0:55 (13)	3:04 ± 4:15 (13)[2]	−3.71 (13)	0.003
Time not incubating (h:mm)[1]	0:54 ± 0:58 (13)	3:05 ± 4:15 (13)[2]	−3.14 (13)	0.009

[1]Data were ln-transformed to achieve normal distribution with equal variances.
[2]Note that only 14 of the 29 birds observed fleeing during first searches also abandoned their nest during second searches (2 failed following first search, 13 stayed).

Effect of cumulative time and frequency of disturbance

Neither the cumulative time a person spent in proximity of a nest (linear regression: $r^2 = 0.005$; $F_{1, 15} = 0.07$; $P = 0.794$) nor the frequency of disturbance (linear regression: $r^2 = 0.01$; $F_{1, 15} = 0.15$; $P = 0.7$) was a suitable predictor for the time a bird was absent from the nest. Despite searchers spending considerably less time in the proximity of the nests (on average 1 h less; Table 4) since most nests had already been recorded and GPS positions had been taken the previous day, the 14 timid individuals (which fled during both searches) abandoned their nest for significantly longer following disturbance by second searches (Table 4).

Discussion

The swift and easy iButton deployment into Fiordland crested penguin nests during first searches had no significant effect on incubation behaviour and disturbance response of the attending bird when compared with nest searches alone. Hence, where video surveillance is difficult, iButtons provide an efficient and practical method to monitor nest attendance patterns while minimising human disturbance impact. Whereas iButton temperature data can confirm if nests remain active after search-related disturbances, events that lead to nest failure cannot be identified and thus must remain speculation. Simultaneous video surveillance and iButton deployment at selected nests should be used to calibrate temperature readings with behavioural patterns.

Nest failure rates due to nest searches

Although searches caused temporary abandonment in almost a third of all nests, the actual failure rate of about 2% per visit was relatively low. iButton data substantiate that while some nests likely failed due to searcher disturbance, others simply failed on the search day and unrelated to human presence.

The time a clutch is left unattended is thought to correlate with the likelihood of nest failure, due to exposure of eggs to the elements or by creating opportunities for predators. For example, human presence at breeding sites resulted in increased predation of Fiordland penguin eggs and chicks by weka (St. Clair & St. Clair 1992). Predators may learn to follow

humans and profit from the distraction they cause (author's personal experiences with stoats in New Zealand, kelp gulls *Larus dominicanus* in Chile, and polar foxes *Vulpes lagopus* in Spitsbergen). In one case the steep decline of temperature after iButton placement suggests that eggs were lost shortly after the bird had left for the first time (cf. Fig. 3b). Experimental data confirm that due to their high thermo-capacity eggs retain temperature and thus buffer the temperature decline following nest abandonment (Ellenberg unpubl. data; cf. Fig. 3a, second absence).

Despite plenty of opportunity created by nest searches, predation pressure currently appears low enough to not affect nest survival significantly, and birds usually return to resume incubation after taking flight.

Penguin disturbance responses depend on timing of nest searches and steepness of terrain

The likelihood of nest abandonment increased when two adults attended the nest, as well as with steepness of terrain, and reduced lateral concealment of the nest.

Search disturbance impact is higher in colonies where nests are still attended by both partners since:

1. Early in the season individual investment into the nest is not yet very high, thus, birds may be more likely to prioritise survival over reproductive success, particularly in long-lived species.
2. There is a 'backup' for the incubating bird in that the attending partner may take over nest defence.
3. No matter if the incubating bird or its partner flees (in the latter case the behaviour would have been recorded as 'stay') fleeing birds may run into and push neighbours off their nest, potentially causing egg loss (observed once).

In order to reduce the likelihood of nest abandonment, good timing of searches is essential. Once clutches are completed penguins spend most of their time in a hunched or prone position, whereas birds attending uncompleted clutches often stand upright on or next to the nest (St. Clair 1992) and thus are more ready to flee. Ideally, the incubation period should be sufficiently advanced so that birds are more inclined to stay. This simple relationship could explain the disturbance impact observed in 2010. The double-count trial on Codfish

Island commenced relatively early (18 August, 11 days prior to nest counts in 2011). In addition, the 2010 breeding season may have been suboptimal. Little penguins (*Eudyptula minor*), for example, had reduced breeding success both in Buller and South Westland (Kerry-Jayne Wilson, West Coast Penguin Trust, pers. comm.).

In contrast to the closely related Snares penguins (*Eudyptes robustus*), whose breeding is highly synchronised (Mattern 2013b), Fiordland crested penguins appear less synchronised in their breeding chronology. Thus, timing of searches needs to be adjusted to reduce disturbance impact.

Nest failures of Fiordland crested penguins due to human presence have been previously reported, but this has never been quantified. St. Clair and St. Clair (1992) noted, 'Early in incubation, when penguins were least tenacious at incubation, our presence in the colonies sometimes made penguins leave their nests temporarily, thereby creating opportunities for Weka predation'. These authors further noted that of 61 nests visited daily only 21 chicks were still alive at the end of the study 6–8 weeks before fledging (St. Clair & St. Clair 1992), but a control area with less intrusive research activities had not been established. In another publication St. Clair (1992) states, 'I discarded the few records for which my disturbance may have facilitated predation', without providing any further information.

During the pre-laying period Warham (1974) observed 'the birds are [now] rather timid and may leave their nests when approached'. Searches early in the breeding season not only increase the likelihood of nest failure, but may also prevent prospecting pairs from establishing nests in the first place (Hockey & Hallinan 1981; Seddon & Ellenberg 2008). Recognising the 'timidity of Fiordland crested penguins' Warham (1974) decided to reduce handling during the incubation and chick-rearing period 'to lessen the risk of losing eggs or chicks'. He did, however, measure egg dimensions and notes that attending males (i.e. single well-established breeders) did stay on the nest, although showing signs of stress (Warham 1974).

Most penguin species show little behavioural reaction to human presence at their breeding sites (Culik & Wilson 1991; Nimon et al. 1995), which is often mistaken for habituation. Evolutionarily this lack of externally manifested stress makes sense; in the absence of land-based predators most penguin populations have not been selected for recognising an approaching human as an immediate threat (Seddon & Ellenberg 2008). Tending eggs or young chicks has absolute priority under often adverse breeding conditions, and leaving the nest may carry a high risk of losing their offspring to conspecific aggression or airborne predators such as skuas (*Catharacta* sp.) or giant petrels (*Macronectes* sp.) (Giese 1996; Descamps et al. 2005). This creates evolutionary selection pressures for steadfast individuals.

Hunting pressure will select for shyer individuals that are cautious of human approach (Riechert & Hedrick 1990; McDougall et al. 2006). Humboldt penguins (*Spheniscus humboldti*), which have been hunted by coastal communities for more than 11 000 years, can be regarded as the most timid penguin species (Ellenberg 2010). Incubating Humboldt penguins respond to humans visible at 150-m distance, and following careful human approach their heart rate needed up to half an hour to return to pre-approach levels (Ellenberg et al. 2006). Similarly, historically hunted yellow-eyed penguins are very wary of human presence, with reduced reproductive output and lower fledgling weights associated with frequent human visitation (Ellenberg et al. 2007, 2013).

Yellow-eyed penguins breed visually isolated in dense vegetation thus they may not have been selected to be particularly steadfast. Despite being the most solitary breeding penguin species (Darby & Seddon 1990), yellow-eyed penguins appear less flighty at their nest sites than Fiordland crested penguins. During nest searches 5% of incubating yellow-eyed penguins fled out of sight (Ellenberg et al. 2009) compared with 11% in Fiordland crested penguins, which regularly leave their nests unnoticed by searchers and clutches routinely get checked to see whether they are still warm, i.e. active.

Species, populations, and even individuals differ in their response to human disturbance for a range of reasons we are just beginning to appreciate. Guarding gentoo penguins (*Pygoscelis papua*), for example, show significantly stronger behavioural responses to pedestrian approach than do guarding king (*Aptenodytes patagonicus*) or royal penguins (*Eudyptes schlegeli*) on the same island (Holmes 2007). Interestingly, the only occasion when the experimental approach resulted in chick abandonment was observed in a king penguin, which is supposedly a species more robust to human disturbance (Holmes 2007).

Observed behavioural responses are only the tip of the iceberg and it is now well recognised that overt behavioural reactions, or the lack of them, are a poor guide to assess human disturbance impact (e.g. Gill et al. 2001; Fernández-Juricic et al. 2005; Wikelski & Cooke 2006). Heart rate measurements of incubating royal penguins, for example, revealed that the current 5-m minimum approach guideline for visitors should be extended to 30 m to exclude potential cumulative effects of human disturbance (Holmes et al. 2005). In comparison, Snares penguins appear essentially naïve to humans and show little behavioural or physiological response to human proximity at their breeding colonies (Ellenberg et al. 2012).

Contrary to skua-mediated systems further south, Fiordland crested penguins can leave their nest sites without the immediate risk of losing their offspring. Furthermore, terrestrial predators may not have been present long enough or in great enough densities in remote Fiordland crested penguin breeding areas to select for more steadfast individuals. Whether the timidity of Fiordland crested penguins is the remnant behaviour of a timid ancestor that has not been counter-selected for or the result of historical hunting pressure currently remains a matter of speculation.

Penguins nesting in steep situations were more likely to flee than birds nesting in moderately sloping or flat habitat. This may in part be due to the often erratic and less predictable movements of humans when searching difficult terrain. There is evidence that penguins make risk-based assessments, treating humans as potential predators (Martín et al. 2004). Thus in order to interpret disturbance responses it is important to understand how dangerous a disturbing stimulus is perceived. Generally, sudden movements or approaching fast is considered more threatening than slow and even movements (e.g. Burger & Gochfeld 1991). Additionally to increased disturbance impact, nest detection rates are generally lower in steep habitat (Hegg et al. 2012) rendering searches of such habitat less relevant for population monitoring.

Finally, lateral concealment was retained in the top-ranking models, i.e. birds in a well-concealed nest were less likely to flee than those nesting in the open. Here it was unimportant if the concealment consisted of vegetation, rock or earth walls. Birds on relatively open nests in grass, on grassy ledges, or rock ledges were generally more flighty than birds in the bush.

Penguins nesting in marginal, often open and suboptimal breeding habitat may be younger, less experienced breeders (Tenaza 1971) or of lower body condition and thus more likely to prioritise survival over nesting success. However, in some cases big males were encountered attending entirely open nests under a high canopy of coastal shrub. Those birds could not only be approached but in some cases even needed to be lifted up slightly to confirm nest contents. This demonstrates clearly that other factors such as individual temperament (e.g. Réale et al. 2007; see below) will also play an important role for predicting the likelihood of taking flight and may explain part of the variability in behavioural responses that remained unexplained by the models. We were unable to quantify individual temperament in this study. However, the largely neglected ecological, evolutionary, and management consequences of animal personality require investigation, particularly in vulnerable and rather timid species such as the Fiordland crested penguin.

Penguin personalities

Warham (1974) has already recognised individual differences and stated 'problems were presented by the timidity of the Fiordland crested penguin, which varies from bird to bird…'. The term personality (also called temperament, behavioural syndrome or stress-coping style) refers to a coherent set of behavioural and physiological stress responses that are consistent over time and that are characteristic of a certain group of individuals (Koolhaas et al. 1999). The decision to stay or flee was highly correlated for individual nests, i.e. birds that fled during the first search were usually flighty during the second search as well. Repeatability of disturbance responses is one of the prerequisites of defining personality, which is thought to be generally consistent over time and situations (e.g. Sih et al. 2004; Réale et al. 2007).

Absences from the nest ranged from 4 min to more than 4 h in nests that remained active throughout the search period. This large range may in part be explained by individual differences in stress-coping styles, i.e. birds that stayed close observing the human intruder needed significantly less time to settle back on the clutch compared with birds that fled for greater distances.

Birds that still fled during second searches, fled greater distances and were absent for longer. However, it needs to be emphasised that only 14 birds of the 27 that had fled during first searches also did so during second searches. The remaining 13 birds decided to stay, probably having classified the searching humans as lower threat following their first encounter. Presumably, only particularly timid individuals continued to flee and probably even became sensitised by repeated disturbance (Ellenberg et al. 2007, 2009). Sensitisation would explain the longer absence times of these birds, whereas the majority of birds appeared less affected by second searches. The potential ecological and evolutionary effects of individual differences in disturbance responses warrant further investigation.

Management implications

Rigorous research can inform and improve management. Double-counts provide considerably more accurate estimates of actual numbers of Fiordland crested penguin nests. Associated disturbance effects can be minimised by searching during the second half of the incubation period when nests are attended by a single, well-established adult. Since onset of breeding can vary considerably between areas, and potentially between years, timing of local search efforts needs to be adjusted accordingly. This may require a pre-search check of a subset of nests to establish stage of breeding cycle. Not only for health and safety concerns of searchers and better nest detection rates, but also to reduce disturbance impact on nesting birds, the colonies chosen for long-term monitoring should contain few truly steep situations. Double-counts may be used to improve the reliability of Fiordland crested penguin monitoring data, provided improved field protocols are used to minimise the effects of human disturbance. Searches will always lead to temporary nest abandonment by some individuals and thus will create predation opportunities. Current predator densities appear low enough not to cause significant nest failure rates. However, this may change in the future, thus predators should be monitored and managed in and around Fiordland crested penguin breeding areas prior to nest searches.

Acknowledgements

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