Factors affecting breeding success of the Flea Bay white-flippered penguin (*Eudyptula minor albosignata*) colony

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Abstract: The little blue penguin (*Eudyptula minor*) is in decline throughout much of its range in New Zealand and Australia, largely due to introduced predators, human disturbance and roadkill mortalities. The white-flippered penguin is a unique morphological variant of the blue penguin, which is traditionally given subspecific status (*Eudyptula minor albosignata*), and is found only on Banks Peninsula and Motunau Island in Canterbury, New Zealand. We monitored a varying number of nest boxes from 1996 to 2009. Overall breeding success was 64% over 13 years of monitoring, with a hatching success rate of 75% and a fledging success rate of 85%. We used a set of generalised linear mixed models and model selection to examine the relative influence of various explanatory variables on hatching, fledging and overall breeding success. Breeding success in nest boxes significantly increased with shorter average pair bond length, longer guard period and later relative lay date. Guard period length was the best predictor of breeding success, followed by relative lay date and average pair bond length. Hatching success also increased with later relative lay date but fledging success was not influenced by any of the explanatory variables measured.

Keywords: Banks Peninsula, blue penguin, *Eudyptula minor*, guard period, lay date, average pair bond length

Introduction

The little blue penguin (*Eudyptula minor* Forster, 1781), or blue penguin as it is often called, is the smallest extant penguin species in the world and the only one that is nocturnal on land (Reilly 1994). The species has a discontinuous distribution around the mainland and offshore islands of southern Australia and New Zealand (Taylor 2000). In Australia, it is patchily distributed along the southern coast from Western Australia to New South Wales on the eastern coast (Davis & Renner 2003). Blue penguins are widespread in New Zealand, and can be found scattered around most coastlines throughout the North Island, South Island and various offshore islands. Six subspecies of *Eudyptula minor* have been recognised (Kinsky & Falla 1976), but their validity has been questioned (Banks et al. 2002), while the white-flippered penguin was considered a full species by Baker et al. (2006). Nevertheless, subspecific names continue to be used by many contemporary authors (e.g. Sagar 2008). The morphologically distinct white-flippered penguin (*Eudyptula minor albosignata* Finsch, 1874) is the subject of this study, and will be referred to here by that name.

The white-flippered penguin is unique to the Canterbury Region (Challies & Burleigh 2004) and breeds only on Banks Peninsula and Motunau Island (Taylor 2000a). Adult white-flippered penguins weigh 0.3 kg more than the 1.0 kg average weight of other blue penguins and their flippers have paler upper-sides and broad white margins (Williams 1995). It has been given a 'nationally vulnerable' threat classification by the Department of Conservation (Hitchmough et al. 2007; Miskelly et al. 2008). While the worldwide conservation of blue penguins may not be a high priority (they are currently listed as 'least concern' on the IUCN Red List), there is a worrying downward trend in local and global populations, which could cause the conservation of blue penguins to become a much larger issue in the long term.

Populations of the little blue penguin have been in decline throughout New Zealand and Australia for a number of years (Dann & Cullen 1990; Challies & Burleigh 2004; Blythe 2007, unpubl. Hons. dissertation; Heber et al. 2008), their decline being attributed largely to predation enabled by a lack of management at mainland colonies (Perriman & Steen 2000; Taylor 2000; Blythe 2007, unpubl. Hons. dissertation). Predation can have a severe impact on breeding success, as both adults and chicks can be taken by predators (Taylor 2000a). This leads to the loss of not only one year's breeding productivity but also future reproductive potential through adults being killed. The combined population size of all white-flippered penguin colonies on Banks Peninsula and Motunau Island was estimated to be 10 460 birds in 2001–2002 (Challies & Burleigh 2004). A total of 1063 active nests were counted at Flea Bay in a 2008 colony census (FWH, unpubl.), reaffirming its status as the largest mainland breeding colony of blue penguins in New Zealand (S. Cashman, unpubl.). Many populations around Banks Peninsula are in serious decline, 83% of nests having been lost from four monitored colonies with 50 nests or more in the last 30 years; one of these colonies has become locally extinct (Challies & Burleigh 2004). However, in a few other colonies on Banks Peninsula (including the Flea Bay colony) populations have been increasing (Challies & Burleigh 2004). In most cases this increase has been attributed to active management, such as predator trapping and nest box installation, or because burrows are largely inaccessible to predators. The population on Motunau Island has also been increasing steadily, probably due to an absence of mammalian predators (Challies & Burleigh 2004). However, an absence of predators does not always result in a healthy and increasing

penguin population, as other factors such as roadkill (Heber et al. 2008), anthropogenic disturbance (Giling et al. 2008), disease (Obendorf & McColl 1980), and poor abundance and quality of food (Dann et al. 2000) can be equally damaging.

Little blue penguins exhibit highly variable breeding success rates and breeding season timing, generally dictated by local conditions. For most colonies in New Zealand (including Flea Bay) the breeding season begins around August and continues until January when chicks fledge at an age of 48–63 days (Davis & Renner 2003). The breeding season generally starts around June in Australia (Priddel et al. 2008) and a June start was reported at Oamaru in the southern South Island of New Zealand (Agnew & Houston 2008). Clutch size is normally two eggs, although clutches of one and three eggs are known, but rare. A second clutch in a single breeding season can also occur in response to a failed first clutch, or in exceptionally good breeding conditions (Davis & Renner 2003), although very rarely at Flea Bay (FWH, unpubl.). Eggs hatch after an incubation period of 33–37 days and chicks are then guarded for the first 20–30 days of the nestling period (Davis & Renner 2003).

Hatching, fledging and breeding success rates are highly variable within and between blue penguin colonies and can be influenced by a wide range of factors. Hatching success is defined as the proportion of eggs that hatch relative to the number of eggs laid, whereas fledging success is the proportion of chicks that fledge relative to the number of eggs that hatch. Overall breeding success is defined as the number of chicks that fledge relative to the number of eggs laid. Factors that have been found to lead to high hatching, fledging or breeding success for pairs or individual birds in Australian blue penguin colonies include better body condition (assessed as mass divided by flipper length) at incubation (Robinson et al. 2005), later relative lay dates (Nisbet & Dann 2009), more sheltered nesting habitat (Knight & Rogers 2004), younger bird age, and longer pair bond length (Nisbet & Dann 2009). When comparing breeding success between colonies, shallow ocean bathymetry (Chiaradia et al. 2007) and lower latitude (Fortescue 1999) have been identified as factors that can lead to increased hatching, fledging or breeding success.

Many biotic and abiotic factors have been identified as potentially having a positive influence on hatching, fledging or breeding success in Australia and New Zealand. However, none of these factors has been tested empirically against any long-term breeding data from a single colony. They include abundant and high quality food supply (Dann et al. 2000), long guard period, short foraging trip duration (Numata et al. 2004; Chiaradia & Nisbet 2006), shallow dive depth when feeding (Chiaradia et al. 2007), high sea surface temperature at various times in the breeding cycle (Mickelson et al. 1991; Cullen et al. 2009), low Southern Oscillation Index values (Perriman et al. 2000), low predation rates (Taylor 2000a), and high burrow and mate fidelity rates (Rogers & Knight 2006).

In the present study we examined whether a number of biotic and abiotic variables affected hatching, fledging and overall breeding success of white-flippered penguins in the Flea Bay colony. By studying a population that is not in decline, a clear idea can be formed as to what factors may influence reproductive success in the absence of those such as predation, roadkill and severe anthropogenic disturbance, which may result in a declining population. This approach is both more responsible, and statistically more robust, than the monitoring of a population in decline. Additionally, 12 of the 18 extant penguin species worldwide are listed as 'near threatened' or worse on the IUCN Red List. Thus, empirical studies of this type may not only provide insight into potential threats to blue penguins and their future management, but other penguin species as well.

Methods

Study site

Banks Peninsula is on the east coast of New Zealand's South Island and was once home to a diverse and abundant native fauna. Flea Bay (43°52' S, 173° 0' E), the site of the present study, is located near Akaroa Harbour on the south-eastern coast of Banks Peninsula (Fig. 1). It makes up the main area of Pohatu Marine Reserve, the only marine reserve on the east
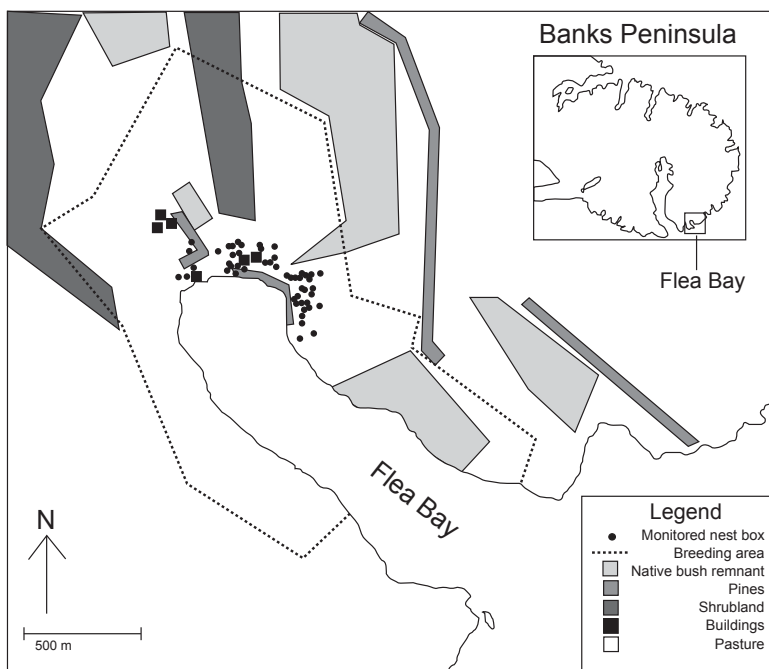

Figure 1. Map showing distribution of monitored nest boxes, approximate breeding area of white-flippered penguins (*Eudyptula minor albosignata*) and broad habitat types at Flea Bay, Banks Peninsula, South Island, New Zealand.

coast of the South Island. However, the bay itself is small, approximately 1.7 km long and 0.35 to 0.5 km wide with about 2.4 km of coastline (S. Cashman, unpubl.). Most of the land surrounding the bay is hilly pasture and shrubland with some moderate-sized coastal forest remnants. The hillsides on either side of the bay are steep (> 45°), whereas land at the head of the bay has a much more gradual slope. The eastern side of the bay has patches of dense native vegetation, whereas the western side has less vegetation, steeper bluffs and is more prone to erosion and slips. Part of the eastern side of the bay is a protected wildlife reserve owned by the Department of Conservation. It has been fenced at times since 2000 to prevent grazing, but is currently unfenced. Cattle graze on the western side of the bay much of the time.

The penguin breeding colony is distributed around much of the Flea Bay coastline (Fig. 1), with most penguins nesting on the eastern side and at the head of the bay (FWH, unpubl.). Penguins nest mainly in natural burrows, although over 300 artificial nest boxes have been provided and are used as an easy way of monitoring penguin breeding. The boxes also provide a measure of protection from large predators such as dogs, and increase the number of nests available to the steadily increasing population.

Breeding data

One of us (FWH) has collected breeding data from artificial nest boxes distributed around the bay (Fig. 1) from the beginning of 1996 to 2009. The same boxes were monitored each year, although the number of monitored boxes increased incrementally from 28 to 58 over the first 7 years of data collection as more were built and installed (Table 1). Each box was checked at intervals of 5–7 days throughout each breeding season and the presence and number of eggs, chicks or adults recorded, along with the band numbers of banded individuals. Most adults were banded when first encountered in a nest box

Table 1. Numbers of white-flippered penguin (*Eudyptula minor albosignata*) nest boxes monitored in 13 breeding seasons at Flea Bay, Banks Peninsula, South Island, New Zealand. Also shown are the numbers of previously banded birds found, and number of birds banded in each breeding season.

Breeding season	Nest boxes monitored	Banded birds found	Birds newly banded
1996/97	28	15	39
1997/98	37	28	39
1998/99	40	50	25
1999/2000	44	51	22
2000/01	48	46	21
2001/02	54	47	33
2002/03	58	46	31
2003/04	58	52	24
2004/05	58	55	30
2005/06	58	65	32
2006/07	58	67	36
2007/08	58	71	32
2008/09	58	73	24

and chicks were banded shortly before they fledged. Banding effort for the monitoring period is summarised in Table 1.

While the effects of nest visitation by researchers and tourists can be hard to quantify, it is known to decrease reproductive success in some penguin species (Giese 1996) and invoke stress responses in others (Fowler 1999; Ellenberg et al. 2006). Penguins that are regularly visited are known to become habituated (Walker et al. 2006) and large-scale regular disturbance of blue penguin colonies visited by unrestricted tourists can lead to nest displacement (Giling et al. 2008). Although disturbance caused by our frequent nest visitations could have had a minor influence on breeding success, the frequency of monitoring was consistent across years.

In some years, pairs of birds had already started breeding when the nest boxes were first checked. In some bird species this can lead to biased breeding success data if breeding attempts (a clutch of one or more eggs being laid) that failed early in the breeding season are missed. However, it is extremely unlikely that failed breeding attempts were missed at Flea Bay for a variety of reasons. Nest boxes containing a breeding pair typically exhibit signs of fresh nest building or renovation, and a build-up of penguin faeces in front of the nest entrance (Davis & Renner 2003). If a nest with these features had no eggs present, this would have been noted in the data as a potentially failed nest. Furthermore, if a nest fails, especially at an early stage, there are almost always signs of failure such as cracked or scattered eggs, egg fragments, a dead chick or other signs of predation (FWH, unpubl.). A sensitivity analysis was also performed to estimate potential effects of missed failed nests by arbitrarily adding a total of 18 failed nests to data from years where birds had started breeding before monitoring began. The sensitivity analysis showed very little change in the *P*-values and regression coefficients for generalised linear mixed models (GLMM) of hatching, fledging and breeding success.

Box–year response measures

Specific annual breeding parameters for each monitored box were calculated for use as response variables in analyses. Hatching success, fledging success and breeding success were calculated as proportional data for each nest box (Table 2).

Box–year explanatory measures

Where banded birds were present, the minimum pair bond length of each breeding pair in each box was recorded. This number was a minimum estimate as some pairs may have been together before monitoring began. The number of parents in their first year of breeding following flipper banding was recorded for each nest box, as foraging behaviour of blue penguins is known to be affected in the first year following banding (Fallow et al. 2009). The lay, hatch and fledging dates (relative to the annual average) of each nest box were also calculated annually. Lay and hatch dates were recorded as the first observation of an egg or chick, respectively. Fledging date was recorded as the first observation where no chick was present in a nest previously occupied by a chick older than 5 weeks and where there were no signs of predation or disease surrounding the nest. If two eggs or chicks in the same nest were laid, hatched or fledged on separate dates, then the average of the two dates was used in analyses. Incubation, guard and nestling period lengths were calculated annually, as above, for each individual nest box. Incubation period was defined as the length of time between the lay date and hatch date. The guard period was the interval between the hatch

Table 2. List of variables, datasets in which they were used, and number of years each variable covered in the GLMM analyses of factors affecting hatching, fledging and breeding success of white-flippered penguins (*Eudyptula minor albosignata*) at Flea Bay, Banks Peninsula, South Island, New Zealand.

Variable	Dataset	Years
Breeding success	Response variable	13
Hatching success	Response variable	13
Fledging success	Response variable	13
MEI annual average	Climate	13
Rainfall total (Sep./Oct./Nov.)	Climate	13
Sea surface temperature (Jun./Jul./Aug.)	Climate	13
Annual cat trap catch	Predators	7
Annual stoat trap catch	Predators	7
Nest box altitude	Nest box characteristics	13
Average pair bond length in nest boxes	Nest box characteristics	13
Nesting habitat	Nest box characteristics	13
Nest box size	Nest box characteristics	13
Nest box aspect	Nest box characteristics	13
Parents in first year breeding after banding	Nest box characteristics	13
Relative lay date	Lay	11
Adult survival	Lay	11
Mate and nest fidelity	Lay	11
Guard period length	Fledging	11
Incubation length	Fledging	11
Nestling period length	Fledging	11
Relative fledging date	Fledging	11
Date of first egg	Fledging	11

date and the first observation of a chick in the nest without an adult present. The nestling period was the number of days between the hatch and fledging dates. In the 2008/09 breeding season, nest boxes were not checked from 16 November to 14 December. Therefore, the lay, hatch and fledging dates, and incubation, guard and nestling period lengths for this breeding season were not used in analyses.

By-box explanatory measures

A number of covariates for each nest box were recorded. The first was internal box size, which was either 300 × 350 mm or 400 × 450 mm. Habitat surrounding each nest box was assigned to one of five categories: pasture, under buildings, shrubland, pine trees, and garden. The slope of the land on which the nest box was placed was assigned to one of four categories (0–5°, 6–20°, 21–35°, >35°), as was the geographic aspect of the land on which the nest box was placed (315–45° = north, 46–135° = east, 136–225° = south, 226–314° = west). Presence or absence of some form of shelter from wind, sun and rain was also noted. The altitude and New Zealand grid map coordinates of each nest box were recorded with a handheld GPS (Global Positioning System, accuracy to ± 5 m). The GPS coordinates were used to calculate the distance of each nest box from the sea with ArcMap in the ArcGIS software suite (ESRI 2008). The turnover rate of pairs in each nest box was calculated as the number of different pairs which bred in each nest box divided by the total number of breeding attempts in that box. The average pair bond length of breeding pairs using each nest box was also calculated using the maximum bond length values for each pair breeding in a particular box. This variable was seen as a measure of nest box quality.

Colony-wide explanatory measures

Several colony-wide variables were measured in each breeding season. The percentage of monitored nests in which breeding was attempted was calculated, and the earliest date an egg was observed in any nest in the colony (not just the monitored nest boxes) was recorded. Monitoring started around the same date each year. An estimate of annual adult survival was calculated as the proportion of banded adults observed in monitored boxes in successive years. This survival parameter is inevitably an underestimate as previously monitored adult birds may have moved to an unmonitored nest box, a natural burrow, or another colony. The colony-wide fidelity rate was calculated as the proportion of breeding attempts in a particular year that involved the same breeding pair in the same nest box as the previous year.

Climate data

We collected climate data used in the analysis from a variety of sources. The Multivariate ENSO (El Niño Southern Oscillation) Index (MEI) was used to approximate changes in broad climatic conditions observed on a monthly basis. The MEI is a principal components analysis (PCA) based on six variables recorded from the Pacific Ocean: sea-level pressure (1), zonal (2) and meridional (3) components of the surface wind, sea surface temperature (4), surface air temperature (5), and total cloudiness fraction of the sky (6) (Wolter & Timlin 1993). It is considered to be an accurate predictor of El Niño and La Niña conditions. Values for the MEI were obtained from the National Oceanic and Atmospheric Administration (NOAA): http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table. html. These MEI values were used to calculate an annual MEI

average, an average for the 3 months before breeding began (June, July, August) and an average for the 3 months during breeding (September, October, November).

Monthly rainfall and air temperature data were obtained from the National Institute of Water and Atmospheric Research (NIWA) CliFlo climate database: http://cliflo.niwa.co.nz. Rainfall data were taken from a weather station at Onuku, Akaroa, about 5 km north of Flea Bay, and air temperature data from Le Bons Bay about 15 km north-east of Flea Bay. Rainfall and air temperature data were used to calculate totals and averages, respectively, for the 3 months before breeding and the 3 months during breeding. Finally, the average monthly sea surface temperature for the entire 13 years was obtained from NIWA. Sea surface temperature data were collected from a buoy off Sumner on the northern coast of Banks Peninsula, 38 km from Flea Bay. Average values for the 3 months before and during breeding were calculated.

Predator data

Trap-catch rates provided by the Department of Conservation were used as a best approximation of abundance of introduced mammalian predators at Flea Bay. A mixture of Fenn (FHT Works, Redditch, UK), DOC 200 (Curtis Metal Products, Auckland, NZ) and Timms (K. B. L. Rotational Moulders, Palmerston North, NZ) traps were used, with a total of 62 traps placed in and around the perimeter of Flea Bay to catch hedgehogs (*Erinaceus europaeus*), stoats (*Mustela erminea*), ferrets (*M. furo*), weasels (*M. nivalis*), cats (*Felis catus*) and rats (*Rattus* spp.). Annual trap catch (per 100 trap-nights) was calculated for each species and the annual catch (per 100 trap-nights) of all species combined was used as a proxy for mammalian predator abundance. Unfortunately, these data only covered the breeding seasons of 2001/02 to 2007/08 and this restricted analysis of predator abundance effects on hatching, fledging and breeding success to seven seasons of data (Table 2).

Data manipulation and analysis

We used a generalised linear model (GLM) to detect significant differences between breeding seasons for the three response variables: hatching, fledging and breeding success. Models were built using R software (R Development Core Team 2008) and assumed a Bernoulli distribution around each year's mean.

Many of the explanatory variables thought to be important in blue penguin breeding success covered only a portion of the 13-year monitoring period, so they were divided into several different datasets (Table 2). This procedure ensured that as many of the breeding data were analysed as possible. Combining all variables into one dataset would have resulted in a much reduced number of breeding seasons being available for analysis, and the removal of explanatory variables could have led to important factors not being recognised.

Within each dataset, explanatory variables were examined for collinearity. When two variables were correlated ($r > 0.35$), only one of the correlated variables was included in the analysis, usually the one most highly correlated to the response variable. Variables dropped from datasets due to intercorrelation were hatch date, distance to sea, land slope, box age, presence or absence of shelter, pair bond length, turnover rate, MEI average (Jun./Jul./Aug. and Sep./Oct./Nov.), rainfall total (Jun./Jul./Aug.), average air temperature (Jun./Jul./Aug. and Sep./Oct./Nov.), average sea surface temperature (Sep./

Oct./Nov.), and total predator trap catch. Hedgehog, ferret, rat and weasel trap catches were all removed from the predator dataset because stoats and cats were considered to be the two most likely predators at Flea Bay.

The final datasets and number of breeding seasons spanned by each explanatory variable selected for analysis are shown in Table 2.

For each dataset, we examined the effects of the explanatory variables on hatching, fledging and breeding success using a GLMM with R software and the lme4 package (Bates et al. 2008). A GLMM was used due to the response variables being proportional data with a binomial distribution, and using a mixed model enabled year to be added to the model as a random effect. Nest box was not included as a random effect because only 28 of the 58 boxes were monitored for the entire duration of the study. Year, nesting habitat, number of parents in their first year breeding following banding, aspect, and nest box size were treated as categorical variables throughout the analysis. Separate analyses were conducted for each of the three response variables as each breeding measure may be influenced by a different combination of explanatory factors.

Full models were constructed for each analysis rather than using a model-building approach. This was done because there were already clear a priori hypotheses formed from the literature regarding what variables may affect hatching, fledging and breeding success. Our approach also allowed us to test each explanatory variable for significance without compromising dataset sample size, but did not allow us to examine the relative importance of significant variables in separate GLMM. Therefore, we also performed a model selection analysis on a single reduced dataset containing the majority of the explanatory variables used in the GLMM, and using breeding success as the only response variable. The data on predator trap catch were removed from this analysis as they covered only 7 years of breeding data and were highly insignificant in the prior GLMM analyses. A balanced (all variables appeared in 15 models) set of 60 models was built based upon a priori hypotheses formed from the literature and derivations of these hypotheses influenced by the results of the GLMM analyses. These models were ranked using Akaike's Information Criterion (AIC) (Johnson & Omland 2004) and the relative importance of variables determined using summed Akaike weights, as recommended by Burnham and Anderson (2002). The results of this model selection process should be interpreted cautiously, however, because of the reduced sample size (301 breeding attempts) compared with the 489 breeding attempts analysed in the largest GLMM.

Results

Breeding success

Over the 13 years of the study there were 489 breeding attempts by white-flippered penguins, with an average of 75% of monitored nest boxes hosting breeding pairs each year. Average colony-wide breeding success over the entire monitoring period was $64 \pm 7.9\%$ (SD; $n = 13$ years) with an average of 1.29 ± 0.84 (SD; $n = 489$ breeding attempts) chicks fledged per breeding pair. Annual breeding success ranged from 53% in the 2002/03 breeding season to 80% in the 2005/06 breeding season (Fig. 2) but did not differ significantly among years in the GLM analysis ($F = 1.21$, $P > 0.265$).

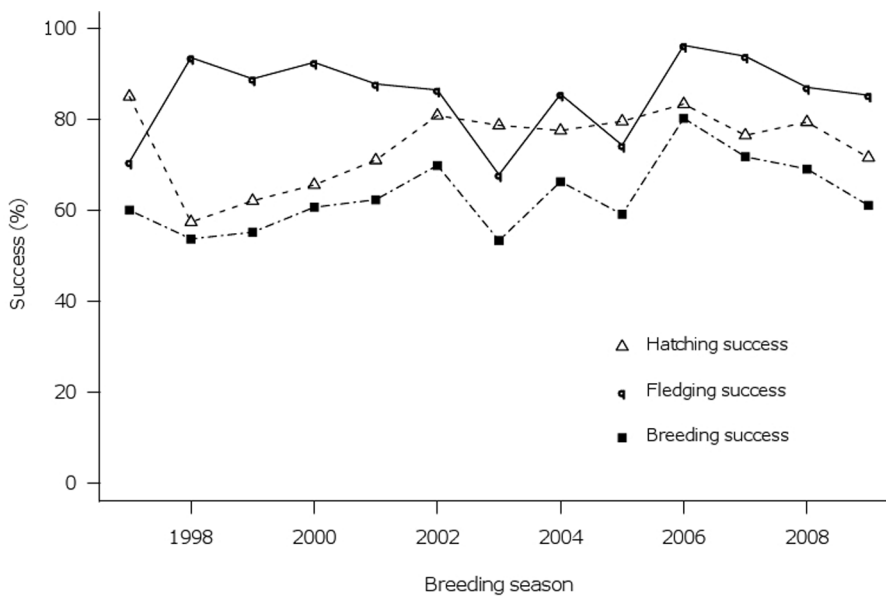Hatching success averaged $75 \pm 8.4\%$ (SD; $n = 13$ years)

Figure 2. Mean annual hatching, fledging and breeding success of white-flippered penguins (*Eudyptula minor albosignata*) in monitored nest boxes at Flea Bay, Banks Peninsula, South Island, New Zealand, between 1996/97 and 2008/09.

with 1.51 ± 0.75 (SD; $n = 489$ breeding attempts) chicks hatched per breeding pair. Hatching success showed similar annual variation to breeding success and ranged from 58% in the 1997/98 breeding season to 83% in the 2005/06 season (Fig. 2). Hatching success between years was also non-significant in the GLM analysis ($F = 1.54$, $P > 0.101$).

Fledging success was high, with an overall average of 85 $\pm 9.0\%$ (SD; $n = 13$ years). An average of 1.53 ± 0.68 (SD; $n = 412$ hatched chicks) chicks fledged per breeding pair that had at least one egg hatch. Fledging success was also variable, the lowest annual average being 68% in 2002/03, the same year in which breeding success was lowest (Fig. 2). In 2005/06 (the best breeding season to date), fledging success was 97%. Fledging success differed significantly among years ($F = 2.09$, $P < 0.014$).

Factors affecting breeding success

Longer guard period ($z = 2.2668$, $n = 314$, $P < 0.0234$: fledging dataset), later relative lay date ($z = 3.4320$, $n = 418$, $P < 0.0006$: lay dataset) and shorter average pair bond length in nest boxes ($z = -1.9793$, $n = 489$, $P < 0.0478$: nest box characteristics dataset) all led to an increased chance of successful breeding as indicated by the GLMM analysis (Table 3). No variables included in the climate or predator datasets were significant predictors of overall breeding success (Table 3).

Relative lay date was the only variable significantly related to hatching success in any GLMM analysis ($z = 2.6843$, $n = 418$, $P < 0.0073$: lay dataset) and none of the explanatory variables examined were significant predictors of the fledging success of the colony.

Results of the model selection analysis showed that breeding success at Flea Bay is most dependent upon length of the guard period. Guard period length was included in all of the top four ranked models (Table 4) and had a summed Akaike weight of 0.57. A value ≥ 0.5 indicates that a variable is likely to be important to the process being investigated (Barbieri & Berger 2004). Conversely, relative lay date and average pair bond length in nest boxes appeared to be relatively unimportant and had summed Akaike weights of 0.24 and 0.19, respectively. Relative lay date only appears in the second, fourth and fifth

most favoured models and average pair bond length in nest boxes in the third and fourth ranked models (Table 4).

Discussion

This is the first detailed study of factors affecting the breeding success of blue penguins in New Zealand using a long-term dataset. We found that breeding success of the white-flippered penguin colony at Flea Bay was dependent upon a number of factors. Longer guard period length, later relative lay date and shorter average pair bond length in nest boxes all led to a significantly increased probability of breeding success. Later relative lay date also positively influenced hatching success.

Guard period length was the most reliable predictor of breeding success in the model selection analysis. During the guard period, both parents take turns (1–2 days at a time) to guard and feed the chick (or chicks) until it can develop its own thermoregulatory capability and start to fend for itself (Numata et al. 2004). When out foraging, a parent must obtain enough food to feed itself and its offspring when it guards the nest. Thus, the length of the guard period is determined by a trade-off between parental investment in the offspring and the parents' own condition and survival. This may make the guard period the most energetically stressful time of the breeding season (Edge et al. 1999). In years or locations with a plentiful and easily obtained food supply, adult body condition will generally be higher, and consequently, the average guard period length will be longer (Numata et al. 2004; Heber et al. 2008).

Higher hatching and overall breeding success at Flea Bay were significantly associated with a later relative lay date, the second most important predictor of breeding success. A later relative lay date was also found to explain higher breeding productivity by individual blue penguins (chicks fledged per breeding attempt) in Australia where breeding productivity increased until around 10 days after the annual average lay date and then began to decrease (Nisbet & Dann 2009). In contrast, the prevailing trend in seabirds is for an earlier relative lay date leading to increased breeding success (Pezzo et al. 2001;

Table 3. *P*-values and regression coefficients (including direction of effect) for each explanatory variable included in five datasets used to examine, using a generalised linear mixed model, breeding success of white-flippered penguins (*Eudyptula minor albosignata*) at Flea Bay, Banks Peninsula, South Island, New Zealand. Bold type denotes significant variables.

Dataset	Explanatory variable	*P*-value	Regression coefficient
Climate	MEI annual average	0.4710	0.7205
	Rainfall total (Sep./Oct./Nov.)	0.7230	−0.3545
	Sea surface temperature (Jun./Jul./Aug.)	0.4960	0.6808
Predators	Annual cat trap catch	0.9011	−0.1242
	Annual stoat trap catch	0.9003	0.1252
Nest box characteristics	Nest box altitude	0.3698	0.8968
	Average pair bond length in nest boxes	**0.0478**	**−1.9793**
	Nesting habitat	0.7758	−0.2848
	Nest box size	0.1433	1.4638
	Nest box aspect	0.4345	−0.7815
	Parents in first year breeding after banding	0.8493	−0.1900
Lay	**Relative lay date**	**0.0006**	**3.4320**
	Adult survival	0.4875	−0.6940
	Mate and nest fidelity	0.1194	−1.5770
Fledging	**Guard period length**	**0.0234**	**2.2668**
	Incubation period length	0.7754	0.2853
	Nestling period length	0.6374	−0.4714
	Relative fledging date	0.4196	0.8071
	Date of first egg	0.7326	−0.3416

Table 4. Factors affecting breeding success of white-flippered penguins (*Eudyptula minor albosignata*) at Flea Bay, Banks Peninsula, South Island, New Zealand. Sixty a priori models were considered and represent a balanced model-set for evaluation of relative covariate importance. Results presented include the explanatory variables in each model, the change in Akaike's Information Criterion (ΔAIC), Akaike weight (w_i) and number of model parameters (n). The top 10 ranked models are shown.

n	Variables in model	ΔAIC	w_i
1	Guard period length	0	0.268
2	Guard period length, relative lay date	1.42	0.132
2	Guard period length, average pair bond length in nest boxes	1.94	0.102
3	Guard period length, relative lay date, average pair bond length in nest boxes	3.37	0.050
1	Mate and nest fidelity	3.97	0.037
1	Relative lay date	4.45	0.029
1	Relative fledging date	4.54	0.028
1	MEI annual average	4.76	0.025
1	Sea surface temperature (Jun./Jul./Aug.)	5.01	0.022
1	Adult survival	5.02	0.022

Paredes et al. 2002). One reason why a later relative lay date may lead to increased breeding success in blue penguins is that adults that forage until later in the season should begin breeding in the best possible body condition because they have been feeding for a longer period of time. Thus, parents may be less energetically stressed during the breeding season, a condition that may lead to increased parental provisioning of chicks and, ultimately, chicks surviving to fledging. Another possible reason is that eggs with a later relative lay date will experience slightly higher initial incubation temperatures and, consequently, higher breeding success rates, a phenomenon observed in crested penguins (*Eudyptes* spp.) by St Clair (1998). Higher relative incubation temperature has the potential to confer an advantage to pairs that lay eggs later in the breeding

season through enhanced development of the chick while in the egg. This may lead to less energetic stress on the parents at later stages in the breeding season (guard and fledgling periods) as chicks are likely to be in good condition when born. In contrast, chick development may be retarded in eggs that experienced lower incubation temperatures (Weinrich & Baker 1978).

Average pair bond length associated with each nest box was the third variable related to breeding success, and was also the third most important parameter identified by the model selection analysis. Breeding success was significantly higher in nest boxes where the average pair bond length of the parents was shorter. Average pair bond length of the occupants of a nest box has not been used in an analysis of breeding

success previously, and its significance may be influenced by its covariance with breeding pair turnover rate ($r = 0.80$). It is possible that penguins compete vigorously for the most desirable nest boxes, resulting in a high turnover rate of pairs, and hence, a shorter average pair bond length. In contrast to average pair bond length in nest boxes, pair bond length of each breeding pair per breeding attempt had no significant effect on breeding success. This apparent contradiction could arise if average pair bond length in nest boxes is an indicator of box quality, rather than a reflection of the length of the pair bond itself. Thus, the quality of nest boxes and natural burrows may be a factor driving breeding success at Flea Bay. Nest box altitude, size, habitat and aspect did not influence breeding success, but more focused research into what factors determine nest box quality would be useful.

No explanatory variables were significantly related to fledging success and only one and three of 21 variables tested in various models were related to hatching and breeding success, respectively. There may be several reasons for the low number of significant variables. Firstly, some explanatory data collected exhibited little variation from year to year (MEI climate data), and secondly, penguins that start breeding almost always persevere through incubation to hatching, even if their body condition is poor (Kemp & Dann 2001; Robinson et al. 2005). Such behaviour would lead to low variation in hatching success rates between nest boxes and breeding seasons. Thirdly, data from artificial nest boxes may not be representative of the colony as a whole. Perriman and McKinlay (1995) and Perriman and Steen (2000) found that breeding success of blue penguins at Taiaroa Head, Otago, was significantly higher in nest boxes than in natural burrows. We do not know if this is also true for Flea Bay, although it is thought that the penguins there also breed slightly more successfully when in a nest box (FWH, unpubl.). If this is indeed the case, then variations in hatching, fledging and breeding success may be lower in nest boxes than in the colony as a whole and thus less likely to show detectable responses to explanatory factors. Finally, intensive management – in the form of predator trapping, care for sick and injured birds, reduced burrow disturbance while nesting, and allowing stock to regularly graze in penguin burrow habitat – was practised at the Flea Bay colony for the entire 13 years of monitoring. Through reducing breeding failure, intensive management may have reduced the effect of some factors that may otherwise explain variation in hatching, fledging or breeding success. For example, intensive trapping of introduced mammals may have almost eliminated predation as a source of mortality of penguin chicks at Flea Bay. All the above factors can be expected to reduce variation in the response and explanatory variables.

In the light of this study, we make a number of recommendations for monitoring and research on white-flippered penguins at Flea Bay. In future, monitored penguins should be implanted with TIRIS[TM] PIT (Passive Integrated Transponder) tags, which appeared to have no detrimental effects when implanted on Adélie penguins (*Pygoscelis adeliae*) (Ballard et al. 2001). This will enable breeding success of individual birds to be examined in depth as done with blue penguins by Nisbet and Dann (2009), as opposed to the success of breeding pairs. PIT tags will also enable individual bird characteristics, such as age or body condition, to be examined as possible factors explaining breeding success at Flea Bay. Measurements of body condition at various times of the breeding cycle may also provide a useful proxy for abundance and quality of food available to penguins. Stationing an automated penguin weighing platform at the base of tracks that penguins with PIT tags are known to use would be one way to achieve this without causing undue stress to birds during the breeding season (Kerry et al. 1993). Knowledge of diet, including preferred prey species, dietary variation from year to year, and foraging sites, is badly needed for blue penguins throughout New Zealand, and should facilitate protection of key habitats away from their terrestrial breeding colonies.

Hatching, fledging and breeding success were mainly high and stable across the 13 years of our study. While this may have confounded our ability to detect environmental factors affecting breeding success, it highlights a positive and encouraging aspect of the study colony: the population of white-flippered penguins at Flea Bay is steadily increasing (FWH, unpubl.). Clearly, blue penguin populations can recover relatively quickly with appropriate management and this bodes well for the future of the Flea Bay and other colonies around New Zealand. The increase in the white-flippered penguin population at Flea Bay is due to the hard work of a small number of people who regard the conservation of little blue penguins as very important, and illustrates how the application of relatively simple measures can provide dramatic benefits for native species.

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