The Journal of Wildlife Management 78(8):1415–1424; 2014; DOI: 10.1002/jwmg.783

Research Article

Evaluation of Artificial Nest Sites for Long-Term Conservation of a Burrow-Nesting Seabird

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ABSTRACT The persistence of many cavity-nesting animals is threatened by habitat modification and a shortage of suitable breeding sites. Consequently, provision of alternative breeding sites is a frequently applied short- to medium-term conservation action. However, the effectiveness of provisioning for breeding success and persistence of breeding animals is rarely considered and could lead populations into an ecological trap. We evaluated the effectiveness of providing nest boxes for little penguins (*Eudyptula minor*) compared with natural nests over 25 years. We assessed nest-box adoption and occupancy rates, compared breeding success (i.e., hatching and fledging success) and indices of productivity (i.e., observed brood size, total fledged chick mass, and the number of clutch initiations) with nest survival models and log-linear mixed effects models, and compared long-term residency patterns with Link–Barker mark-recapture models between artificial and natural nests. Little penguins readily adopted nest boxes and breeding attempts were recorded in about 92% of nest boxes installed for 7 or more years. Breeding productivity from 6,081 monitored clutches varied by year and was similar across nest types in most years, but in poor breeding seasons nest boxes performed better. Survival rates to hatching and fledging averaged 7.6% and 8.6% greater in nest boxes, respectively. Similarly, the average total observed mass of chicks produced per clutch was 11% heavier in nest boxes. Annual site fidelity of 2,331 breeding penguins was similar in areas with nest boxes and areas with natural burrows, despite an average of 35% of natural burrows collapsing each year. Nest-box provisioning for little penguins overcomes local nest-site limitation, improves breeding success, and can result in local population increases, so is not indicative of an ecological trap. However, a self-sustaining local population in the long term will require management strategies that address the underlying processes inhibiting population recovery and assist the transition from artificial nest sites back to natural nest sites. © 2014 The Wildlife Society.

KEY WORDS artificial nest boxes, Australia, breeding performance, ecological traps, *Eudyptula minor*, little penguins, mark-recapture, site fidelity.

Limited breeding site availability is a primary threat to the conservation of many animal populations and considerable effort is given to restoring key habitat features that facilitate population maintenance and recruitment (Newton 1994*a*, Lindenmayer et al. 2009). Limitation of suitable sites for breeding may result from habitat modification or elevated clutch predation, and providing artificial breeding sites may reduce these impacts (Newton 1994*b*, Pöysä and Pöysä 2002, Griffith et al. 2008, Catry et al. 2009, Vaclav et al. 2011). However, the effectiveness of providing artificial nest sites, relative to natural nest sites, is rarely considered (for exceptions see Fargallo 2001, Llambias and Fernandez 2009, Libois et al. 2012). Furthermore, responses of populations following provision of artificial nest sites may not be monitored over enough generations to determine any long-term consequences (though see Catry et al. 2009, Libois et al. 2012).

A risk of nest-site provisioning is that populations can fall victim to an ecological trap where artificial nest sites are preferentially used by the target population but confer inferior breeding productivity or survival, effectively representing a population sink and undermining long-term population recovery (Gates and Gysel 1978, Kokko and Sutherland 2001, Schlaepfer et al. 2002), which has been observed in nest-site provisioning programs (Mänd et al. 2005, Klein et al. 2007, Rodriguez et al. 2011). To ascertain whether artificial nest sites are effective in the long term they must be readily adopted by the target species, breeding success must be comparable with natural nest sites over many years, artificial nest sites must have comparable adult residency rates as natural nest sites, and ideally the population must transition to natural nest sites once habitat restoration or predator control is achieved.

Received: 9 May 2013; Accepted: 15 July 2014
Published: 29 September 2014

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We assessed the short- and long-term effectiveness of nest-site provisioning for a burrow-nesting seabird, the little penguin (*Eudyptula minor*). Little penguins are the smallest species of penguin and resident breeding colonies are distributed across New Zealand and southern Australia (Marchant and Higgins 1990). The colony on Summerland Peninsula, Phillip Island, Victoria, Australia is the last remaining of 10 colonies on Phillip Island. The 9 colonies lost during the 20th century were smaller and succumbed to breeding habitat loss as a result of urbanization and predation by foxes (*Vulpes vulpes*) and dogs (*Canis familiaris*; Dann 1992). Subsequent predator control and habitat reclamation has allowed the colony on Summerland Peninsula to expand over the last 3 decades to about 30,000 breeding penguins (Sutherland and Dann 2012, 2014).

Nest boxes have been installed elsewhere for the conservation of penguins with mixed success. Little penguins have successfully bred in nest boxes in Western Australia (Klomp et al. 1991) and New Zealand (Houston 1999, Perriman and Steen 2000, Braidwood et al. 2011), but where breeding success was compared with natural burrows, performance was less than or equivalent to that at natural burrows. None of these studies monitored performance for multiple consecutive generations. Yellow-eyed penguins (*Megadyptes antipodes*) were able to recolonize and breed on farmland that was formerly coastal forest after nest boxes were established (Lalas et al. 1999). Nest boxes provided the equivalent structural cover of dense vegetation and were preferred to natural sites, though breeding success was not compared with a population reliant on natural nests. Breeding success of African penguins (*Spheniscus demersus*) was improved after provision of nest boxes that compensated for the loss of guano-rich soils in which burrows could be excavated (Sherley et al. 2012).

Our aim was to determine the long-term effectiveness of providing nest boxes as a management tool for conserving local populations of breeding little penguins from 25 years of nest-site provisioning and monitoring. If nest boxes for penguins act as an ecological trap, they are an ineffective management tool and potentially undermine conservation objectives. Thus, to examine this possibility we 1) determined the rate at which nest boxes were adopted by penguins and used for breeding (hereafter, uptake rate); 2) compared breeding success between artificial and natural nest sites; and 3) compared residency patterns of breeding penguins at natural burrows with those at nest boxes. High uptake rates of nest boxes combined with either lower breeding success or lower adult survival are indicative of an ecological trap.

STUDY AREA

This study was conducted on Summerland Peninsula (Dann 1992, Sutherland and Dann 2012) on the western end of Phillip Island, Victoria, Australia (38°30′S, 145°9′E; Fig. 1). The peninsula is a plateau surrounded by a rocky shoreline and sandy beaches, and dominated by blue tussock grass (*Poa poiformis*), bower spinach (*Tetragonia implexicoma*), and seaberry saltbush (*Rhagodia candolleana*). Little penguins return to the peninsula from foraging trips at sea to breed in burrows excavated in the sand and loam soils, under vegetation, in rock crevices or under buildings (Stahel and Gales 1987). The primary predators of eggs and chicks over the years have been foxes and little ravens (*Corvus mellori*; P. Dann, Phillip Island Nature Parks, unpublished data).

Breeding habitat on the peninsula has been significantly modified since European settlement in the 1840s. Grazing was initiated in the 1840s, and in 1927 a 776-lot Summerland Estate was established on the eastern half of Summerland Peninsula. The development of this estate significantly altered the environment by clearing vegetation, introducing weeds, compacting soils, and introducing other threats such as vehicles and domesticated carnivores (Dann 1992). Concurrent with this development, the nightly parade of penguins crossing Summerland Beach at the eastern edge of the colony (henceforth termed the Penguin Parade) became increasingly popular for visitors wishing to see this natural spectacle. In 1985 the Victorian State Government bought back the entire Summerland Estate with the objective of returning the peninsula to habitat for wildlife. This was completed in 2010 with the removal of the last of 190 buildings. Nest boxes were installed beginning in 1981 to counter breeding habitat loss and declining densities of breeding penguins in some parts of the colony.

We established 6 study areas to monitor use of natural burrows and nest boxes (Fig. 1). These comprised 3 study areas with only nest boxes, 2 of these in the Summerland Estate and 1 at the Penguin Parade; 1 study area comprising a combination of natural and artificial nest sites; and 2 study areas with only natural burrows. Study areas were about 0.5 ha in size, though nest boxes in the housing estate study areas were distributed in clumps over about 5 ha and 20 ha.

METHODS

Artificial Nest Boxes

We constructed nest boxes of treated pine with an open base (W450 × D450 × H300 mm), a square-entrance tunnel (150 mm on a side) projecting from 1 side, and a removable lid to facilitate nest inspections. A similar design also has been used elsewhere for little penguins (Klomp et al. 1991, Fortescue 1995, Houston 1999). We partially buried nest boxes or mounded soil on the sides to reduce internal burrow temperature and placed boxes in mounds of sand to facilitate drainage in habitats where the clay content of the soil was high. We also planted indigenous plant species nearby to provide shade. When buildings were removed in the housing estate, we mapped the existing nest sites on each block, and after demolition or removal of the building, we placed nest boxes at the original nest sites. We added extra nest boxes nearby in case the original nesting sites were no longer acceptable. Houses were removed during the non-breeding season when most penguins were out at sea (Dann et al. 2000). We also installed nest boxes in instances where other infrastructure or habitat restoration activities were conducted that displaced nest sites.

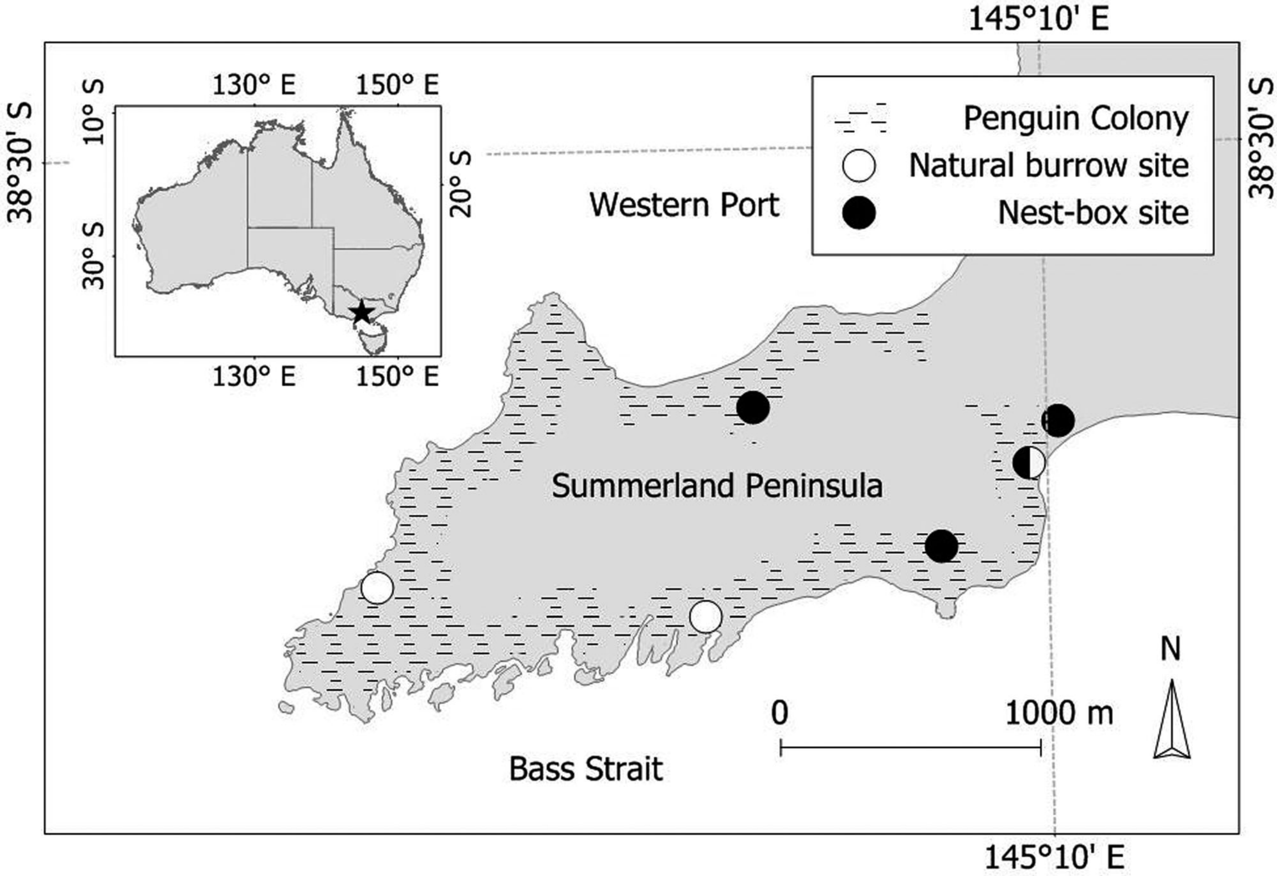

Figure 1. Location of Phillip Island, Australia, indicated by the star, and distribution of the little penguin colony and study areas on Summerland Peninsula on the western end of Phillip Island.

Nest-Site Monitoring

We installed wooden nest boxes in the study areas within the Summerland Estate between Jun 1986 and Oct 1990. Nest boxes in the Penguin Parade area were first installed in 1981, but unlike in the housing estate, the date that most nest boxes were installed in this area was not recorded. Biweekly monitoring of artificial and natural nests from laying through chick fledging commenced in the breeding season of 1986 and 1987 except in the Penguin Parade where we monitored nest boxes every 4 weeks from 1986 to Jun 1990, and biweekly from Jul 1990 to Jun 2011. We aimed to monitor a relatively constant number of natural burrows within study areas between years.

Breeding in little penguins at Phillip Island usually occurs in the Austral spring and summer between August and February (Nisbet and Dann 2009). Little penguins incubate 2 eggs of equal size for about 35 days (Kemp and Dann 2001) and return to feed their chicks for another 55 days or more before the chicks fledge (Reilly and Cullen 1981, Chiaradia and Nisbet 2006). We individually marked all adult penguins with flipper bands prior to 2000 and progressively removed and replaced bands with passive integrated transponder (PIT) tags thereafter. We captured chicks and weighed them to ±10 g using a spring scale (2 kg Super Samson, Salter Brecknell, Smethwick, UK) during each nest visit and marked them either with flippers bands once they reached about 700 g in weight and obtained adult plumage, or with PIT tags beginning in 2000. Chicks are only likely to fledge once reaching at least 700 g (Chiaradia and Nisbet 2006) and the monitoring protocol meant few if any chicks at study areas fledged without being marked. All procedures were approved by the Phillip Island Nature Park Animal Ethics Committee (1.94, 1.97, 7.2000, 2.2003, 6.2006, and 3.2008), Australian Bird and Bat Banding Scheme License (8004), and Victorian Department of Sustainability & Environment Animal Use Permits (10003374, 10004863 and 10005238).

Breeding Success

We estimated the success rates of penguins incubating at least 1 egg to hatch (hereafter, hatching success) and then brooding and provisioning chicks to fledge (hereafter, fledging success) using nest survival models (Dinsmore et al. 2002, Rotella et al. 2004). These models are useful where nesting sites are monitored only periodically so that nest initiation and failure are not actually observed for most nests. Failing to account for this uncertainty can bias hatching and fledging success estimates (Mayfield 1975). We considered nest or brood failure to have occurred when all eggs or chicks failed in a clutch. We considered hatching and fledging success rates to vary in response to 3 factors, nest type (nest boxes or natural burrows), study area, and year. Because nest type and study area were largely confounded, we treated them as competing hypotheses to explain geographic variation in the data. That is, we did not include both terms in the same model. We constructed competing models in R (version 2.15.3, R Core Team 2013) using the package RMark (version 2.1.4, Laake et al. 2012), which calls upon program MARK (version 6.1, White and Burnham 1999). We evaluated model fit using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We selected models with $\Delta AIC < 2$ as best supported models, and where model selection uncertainty existed, we model averaged parameter estimates (Burnham and Anderson 2002).

We included data from Jul 1994 to Jun 2011 in the models because prior to Jul 1994, empty nest sites were not routinely recorded as empty, hence we were unable to distinguish whether nests had not been checked or were in fact empty, which could influence the output from nest survival models. In most years, breeding began after Jul and finished by Mar prior to adults molting (Reilly and Cullen 1983). However, in 1991, 1992, 2000, 2001, and 2010 we observed eggs and chicks earlier, so we considered years to begin on the first day of Apr each year. We considered hatching successful if the nest was active on the previous visit and we later observed the chicks or at least 35 days had passed since we first recorded the eggs. If chicks were absent after 35 days then we considered this chick failure. We assumed chicks had fledged only if they were alive in the previous check, and if at least 55 days had passed since the chick was first observed or 90 days had passed since the egg was first observed (Chiaradia and Nisbet 2006). This approach distinguishes some level of hatching and fledging success (1 or more chicks hatched or fledged) from complete nesting failure. To explain the variation in hatching and fledging success rates, we compared 10 models based on the factors described above: nest type, study area, and year (Table 1). We present 85% confidence intervals around parameter estimates to be consistent with the level of significance associated with AIC model selection (Arnold 2010).

Productivity Indices

We also sought to compare breeding success in natural and artificial nest sites using observed indices of productivity, rather than using nest survival models, in each year from 1988 to 2010 because using observed success will be comparable with other studies (Perriman and Steen 2000, Barham et al. 2007, Heber et al. 2008, Hervías et al. 2013) that have not employed nest survival models and because it allowed us to distinguish between full and partial nesting success. Not all study areas had sufficient nests being checked prior to 1988 to use nest survival models. This approach also contrasts with the nest survival modeling approach in that the resulting survival rates will effectively miss breeding attempts that failed before nests were first monitored or failed after the last monitoring occasion and hence these indices suffer some bias. We used 3 indices of productivity: 1) the observed number of eggs hatching from each initiated clutch (i.e., observed brood size); 2) the sum total of chick mass measured from all fledged chicks in each clutch within a year (i.e., chick mass); and 3) the number of clutches laid at each nest per year (i.e., clutch initiations). Observed brood size is an index of hatching success that reflects the amount of reproductive success of each clutch (i.e., beyond whether none or at least 1 egg hatched per clutch). We treated fledged chick mass as an index of fledging success, rather than number of chicks fledged, because it captures instances when 2 chicks successfully fledged per clutch, and because heavier chicks are more likely to survive (Reilly and Cullen 1982). We included the number of clutches laid per year at each natural or artificial nest as an index of productivity because hatching or fledging success for the year is the product of the success rate per clutch and the number of clutches.

Similar to our hatching and fledging success analyses, we examined the effects of nest type (artificial or natural) or study area, year, and the interaction between nest type or study area and year on apparent breeding success metrics using generalized linear mixed models with either a Poisson distribution (for observed brood size and clutch initiations) or a Gaussian distribution (for clutch mass) constructed in R using the lmer function in package lme4 (version 1.0–4; Bates et al. 2013). Because breeding attempts could be repeated at the same nest within and between years, we included nest identifications as random intercepts in productivity models (Zuur et al. 2009). We examined all possible model combinations ($n = 8$ models) for each index with AIC_c. We visually assessed residuals of the most supported models for homogeneity of variance and independence.

Residency

We estimated the residency of individual penguins breeding from 1988 to 2010 by calculating apparent survival and re-sighting rates of breeding penguins using Link–Barker

Table 1. Ranked list of nest survival models from program MARK to estimate daily nest survival, *S*, of little penguins during egg incubation (hatching success) and chick rearing (fledging success) in nest boxes and natural burrows at 6 study areas on Phillip Island, Australia, from 1994 to 2011. Models included effects of year (year), type of nest (nest; artificial or natural), and study area (area). Models are ranked by Akaike's Information Criterion adjusted for small sample sizes (AIC_c); differences from the top ranked model (ΔAIC_c), number of parameters in each model (K), AIC_c weight (ω_i), and model deviance are presented for models with $\omega_i > 0.05$. Monitored clutches: incubation $n = 6{,}081$; chick rearing $n = 4{,}056$.

Breeding stage	Rank	Model description	K	ΔAIC_c	ω_i	Deviance
Hatching success	1	S (year + nest + year × nest)	34	0^a	0.836	10,208.91
	2	S (year + nest)	18	3.94	0.116	10,244.87
Fledging success	1	S (year + nest + year × nest)	34	0^b	0.607	7,750.74
	2	S (year + nest)	18	0.87	0.392	7,783.62

[a] $AIC_c = 10{,}276.93$.

[b] $AIC_c = 7{,}818.75$.

models (Link and Barker 2005) constructed in the R package RMark. For each year starting in April, we defined breeding penguins as adults observed at a nest with either an egg or chick. This approach measures residency patterns by tracking the fate of individual penguins rather than individual nest sites and so follows penguins moving between burrows within a study area. This approach cannot account for breeding penguins moving off-area or into unmonitored burrows.

Link–Barker models estimate the per capita probability of penguins immigrating to a study area or returning to natal or previous breeding areas (recruitment or fecundity, f), the probability then of surviving and being present at the same study area the following year given losses from emigration and death (or apparent survival, φ), and the probability of re-sighting penguins (p) the following year, which incorporates the detectability of penguins given our nest-site monitoring protocol and the temporary departure of individuals from study areas (akin to definitions in Schaub et al. 2001). Again, similar to our breeding success analyses, we developed competing models considering either nest type or areas to best explain the data. First, we considered combinations of models with nest type influencing residency. We considered φ, p, and f each with 6 possible sub-models: year, year + nest type, year + sex, year + nest type + sex, year + nest type + year × nest type (an interaction between year and nest type), and year + nest type + sex + year × nest type. We did not consider any models with an interaction term in more than 1 of φ, p, or f to minimize over-parameterization, but the interaction term allowed residency patterns to vary independently between years and nest types. All models considered φ, p, and f varying with time because we expected colony attendance patterns to vary among years for little penguins (Nisbet and Dann 2009). We considered models with and without sex because sex also is likely to influence attendance patterns (Nisbet and Dann 2009). Second, we considered the same set of models again but with study area replacing nest type as a factor. We compared the combined set of 320 unique models using AIC_c as described previously. From the most supported model we derived population growth rates (λ) from recruitment and survival rates to compare between nest types.

RESULTS

Over 25 years, we monitored a median of 52 and 127 nest boxes in the 2 study areas within the Summerland Estate, 38 nest boxes at the Penguin Parade study area, 22 nest boxes and 19 natural burrows at another study area near the Penguin Parade, and 39 and 46 natural burrows at 2 additional study areas (Fig. 1).

Nest Box Uptake

Nest boxes in the Summerland Estate were readily accepted by penguins. In their first year after installation, 65% of nest boxes were occupied and 81% of those were used for breeding, reaching an asymptote of 97% occupied and 93% breeding after about 7 years (Fig. 2). Not every burrow was occupied each year and not every occupied burrow was used for breeding by penguins each year. All burrows were occupied by breeding penguins at least once during the study, but 9% of nest boxes were used for breeding in less than 10% of the years in which they were installed.

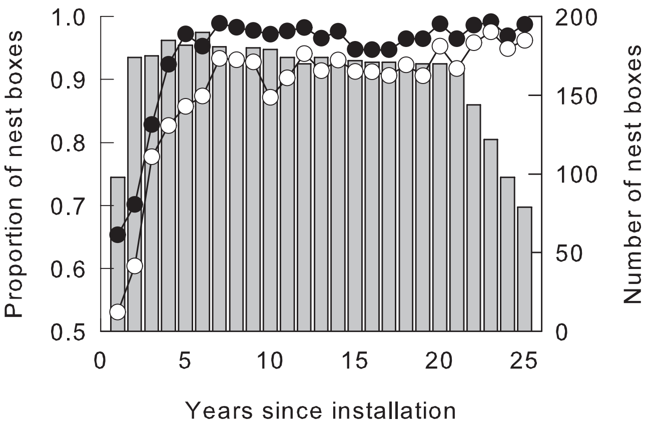

Figure 2. Proportion of nest boxes installed on Phillip Island, Australia, occupied (black circle) and used for breeding (white circle) by little penguins since the nest box was installed. The number of nest boxes monitored (bars) increased as more nest boxes were installed. In the most recent years, fewer nest boxes had been installed early enough to be monitored for 22 years or more.

Breeding Success

The hatching success of 6,081 monitored clutches (270–441 per year) was generally greater in nest boxes (mean $\varphi = 0.66$; CI = 0.62–0.71) than natural burrows (mean $\varphi = 0.59$; CI = 0.51–0.66), but differences were evident only in some years. Hatching success was less variable between years in nest boxes than natural burrows and differences seemed to arise when success was below average in natural burrows (Fig. 3). The most supported models included nest type and year effects and their interaction. Alternative models considering variation between study areas rather than nest types were less supported (Table 1).

Of the 4,056 nesting attempts where at least 1 egg hatched, the frequency of chicks fledging after 55 days was greater for nest boxes (mean $\varphi = 0.68$; CI = 0.63–0.73) than natural burrows (mean $\varphi = 0.60$; CI = 0.51–0.67), but confidence intervals overlapped in all but 5 years of the study when fledging success was below average in natural burrows (Table 1; Fig. 3). Catastrophic nest failure at both natural burrows and artificial nests in 1997 was due to a mass mortality of pilchard (*Sardinops sagax*), a significant prey species for penguins (Dann et al. 2000, Chiaradia et al. 2010).

Productivity Indices

Indices of resulting brood size from all attempted clutches, whether successful or otherwise, did not differ between natural burrows and nest boxes but did differ among study areas (Table 2; Fig. 4). This result contrasts with the result above (breeding success) that penguin clutches in nest boxes were more likely to hatch at least 1 egg than natural burrows.

The total mass of chicks per clutch observed to fledge was generally greater in nest boxes than natural burrows, but confidence intervals overlapped in all but 6 years of the study

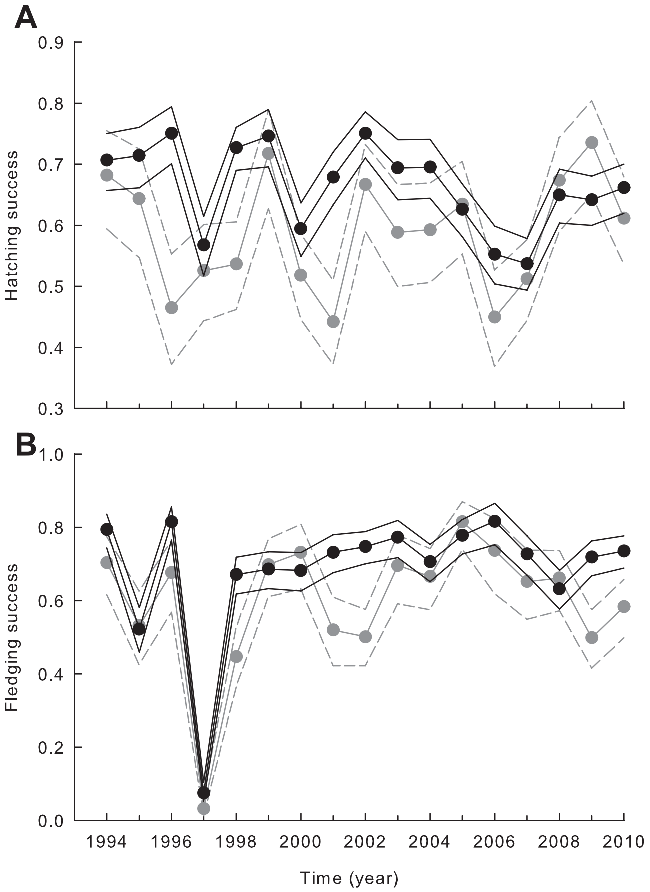

Figure 3. (A) Mean hatching success rates over 35 days, and (B) mean fledging success rates over 55 days with 85% confidence intervals for little penguins in natural burrows (grey symbols) and nest boxes (black symbols) over 17 years on Phillip Island, Australia as estimated by model averaged nest survival models in program MARK.

(Table 2; Fig. 4). On average, fledged clutches were 11% heavier when they hatched in nest boxes (mean = 832 g; CI = 757–908 g) than if they hatched in natural burrows (mean = 740 g; CI = 624–858 g). The number of clutch initiations at burrows varied among years but was similar between natural and artificial burrows (mean = 1.20 clutches per nest; CI = 1.11–1.29).

Residency

We compared residency patterns through time of 2,331 marked adult penguins. The most supported model included nest type as a factor rather than study area (Table 3). Models including study area as a factor were not well supported ($\Delta AIC_c \geq 18.44$). The most supported model suggested that penguins breeding in areas with natural burrows had a similar mean rate of apparent survival ($\varphi = 0.78$; CI = 0.74–0.80) to areas with nest boxes ($\varphi = 0.77$; CI = 0.71–0.82), but survival rates were more consistent between years in artificial nests (Fig. 5A). Male penguins had a slightly higher apparent survival rate overall ($\varphi = 0.78$; CI = 0.74–0.82) than females ($\varphi = 0.77$; CI = 0.72–0.81), but this difference was not biologically meaningful.

The probability of re-sighting breeding penguins differed between nest types and sexes. Re-sighting rates were on average 18.4% greater at nest boxes ($p = 0.79$; CI = 0.77–0.81) than natural burrows ($p = 0.60$; CI = 0.57–0.64). This indicates that penguins were less likely to temporarily leave nest boxes, probably reflecting the greater longevity of nest boxes compared with natural burrows. Less than 1% of nest boxes collapsed per year and most were repaired or replaced, whereas about 35% (SD = 17%) of natural burrows collapsed each year (Fig. 6). Furthermore, average re-sighting rates were 3.4% greater for males ($p = 0.72$; CI = 0.69–0.74) than for females ($p = 0.68$; CI = 65–71), which is consistent with the observation that males have greater nest-site fidelity as they establish and seek to attract partners to their burrow (Reilly and Cullen 1981). Little penguin population growth rate (λ), which is the sum of recruitment rates and apparent survival rates, differed between nest types, study areas, and years. Growth rates were greater at artificial nest boxes ($\lambda = 1.04$; CI = 0.99–1.09) than natural burrows ($\lambda = 1.00$; CI = 0.94–1.08), though this varied among years and confidence intervals overlapped broadly (Fig. 5B).

DISCUSSION

Nest boxes are an effective management tool for the local conservation of little penguins as evidenced by the high rate of nest-box uptake; by the similar overall reproductive output in nest boxes and natural burrows in most years, but when breeding success is relatively poor in natural burrow, artificial nest boxes perform better; and by greater site fidelity of

Table 2. Ranked list of log-linear mixed effects models to explain the number of little penguin eggs observed hatching per clutch attempt (brood size), total mass of little penguin chicks successfully fledged per clutch (chick mass), and the number of little penguin clutches attempted (number of clutches) in nest boxes and natural burrows at 6 study areas on Phillip Island, Australia, from 1986 to 2011. Models included or omitted effects of year (year), type of nest (nest; artificial or natural), and study area (area). All models included a random factor of individual nest identification. Models are ranked by Akaike's Information Criterion adjusted for small sample sizes (AIC_c); differences from the top ranked model (ΔAIC_c), the number of fixed parameters in each model (K), AIC_c weight (ω_i), and model deviance are presented for models with $\omega_i > 0.05$. $n = 8{,}183$ monitored clutches.

Breeding stage	Rank	Model description	K	ΔAIC_c	ω_i	Deviance
Brood size	1	year + area	29	0[a]	0.986	21,181.6
Chick mass	1	year + nest + year × nest	56	0[b]	1	127,057.6
Number of clutches	1	year	24	0[c]	0.647	17,751.6
	2	year + nest	25	1.45	0.313	17,751.0

[a] $AIC_c = 21{,}239.8$. All other models had $\omega_i < 0.01$.

[b] $AIC_c = 127{,}154.2$. All other models had $\omega_i < 0.01$.

[c] $AIC_c = 17{,}799.7$.

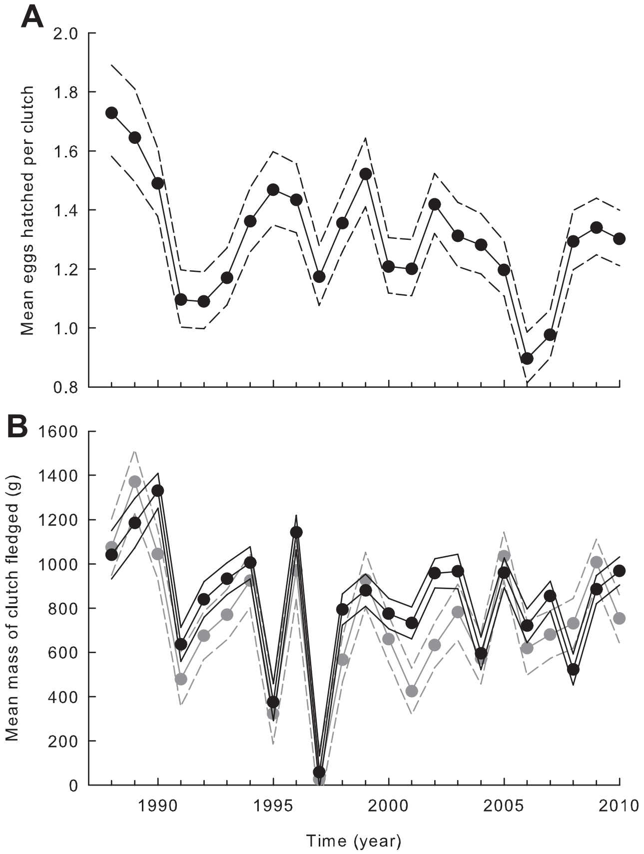

Figure 4. (A) Mean number and 85% confidence intervals of little penguin eggs observed hatching per clutch in each year from 1988 to 2011 on Phillip Island, Australia, (the most supported model suggested no difference between artificial and natural nest types), and (B) mean total mass per clutch observed fledging in natural burrows (grey symbols) and nest boxes (black symbols) as estimated from model averaged log-linear models.

penguins in areas with nest boxes than with natural burrows. Greater breeding success at artificial nest sites is consistent with many bird studies evaluating nest-site provisioning (Fargallo 2001, Bolton et al. 2004, Catry et al. 2009, Llambias and Fernandez 2009), a pattern which has encouraged the use of nest boxes for the conservation of populations. For example, Madieran storm petrels (*Oceanodroma castro*) in the Azores islands had 2.9 times greater breeding success in nest boxes than in natural nest sites, leading to an increased local population size (Bolton et al. 2004). However, this contrasts with findings from a number of studies where artificial nest sites were preferentially used but resulted in lower chick survival or breeding success (Pöysä and Pöysä 2002, Mänd et al. 2005, Klein et al. 2007, Rodriguez et al. 2011). In Spain, Eurasian rollers (*Coracias garrulus*) preferentially used more visible nest boxes, but breeding success was significantly lower (Rodriguez et al. 2011). Nest boxes in several instances were able to increase the density of breeding adults, but were then associated with reduced breeding success. Nest boxes stimulated supra optimal breeding densities of great tits (*Parus major*) in preferred habitats, which was associated with significantly reduced breeding success, whereas in non-preferred habitat, birds were unable to exploit the breeding habitat fully despite additional breeding sites (Mänd et al. 2005). Such scenarios indicate an ecological trap (Gates and Gysel 1978, Kokko and Sutherland 2001, Schlaepfer et al. 2002), precipitating a net population decline, which is clearly counter to conservation objectives. Our results are not consistent with nest boxes creating an ecological trap for little penguins.

Several explanations can be proposed for why nest boxes were attractive for little penguins. First, establishing nest boxes may confer lower energetic costs relative to excavating natural burrows. The energetic cost of constructing natural burrows is unknown but is expected to be considerable and may be compounded over an individual's lifetime as natural burrows collapse. Second, nest boxes may be attractive because nest-site availability is limiting (as in Pöysä and Pöysä 2002, Vaclav et al. 2011). Nest sites were clearly limiting in some areas prior to the installation of nest boxes as no breeding penguins were present beforehand, possibly because the soils were compacted and unsuitable for burrowing. Third, nest boxes may be attractive because penguins considered nest boxes as greater quality nesting sites, whether this is driven by thermal properties, space, or location. The proportion of nest boxes in this study that were occupied, and in which breeding was attempted, continued to increase for about 7 years, after which time it remained relatively constant (Fig. 2). This corresponds with a long-term study of nest box uptake for a tree-nesting species (Corrigan et al. 2011) suggesting that although initial uptake of nest boxes may be high, peak uptake for many species could take several years and may be underestimated in shorter studies.

Greater recruitment rates shown at artificial nest boxes in our study are most likely due to the initial influx of penguins to areas when nest boxes were first installed, but also due to

Table 3. Ranked list of Link–Barker mark-recapture models to describe residency patterns of breeding little penguins at 6 study areas on Phillip Island, Australia, between 1988 and 2011. Included are the most supported models based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c). Differences from the top ranked model ($\Delta\mathrm{AIC}_c$) are presented with their number of parameters (K), AIC_c weight (ω_i), and model deviance for models with $\omega_i > 0.05$. Models include the influence of year (year) or study area (area), sex (sex), and nest type (nest) on apparent survival (φ), the probability of re-sighting individuals (p), and rate of appearing on study areas (f). Effective sample size = 17,039 detections.

Rank	Model description	K	$\Delta\mathrm{AIC}_c$	ω_i	Deviance
1	φ (year + nest + sex + year × nest) p (year + nest + sex) f(year + nest + sex)	94	0^a	0.53	14,642.9
2	φ (year + nest + year × nest) p (year + nest + sex) f (year + nest)	92	5.00	0.23	14,651.9
3	φ (year + nest + year × nest) p (year + nest + sex) f (year + nest + sex)	93	5.70	0.15	14,650.6

[a] $\mathrm{AIC}_c = 66{,}944.8$.

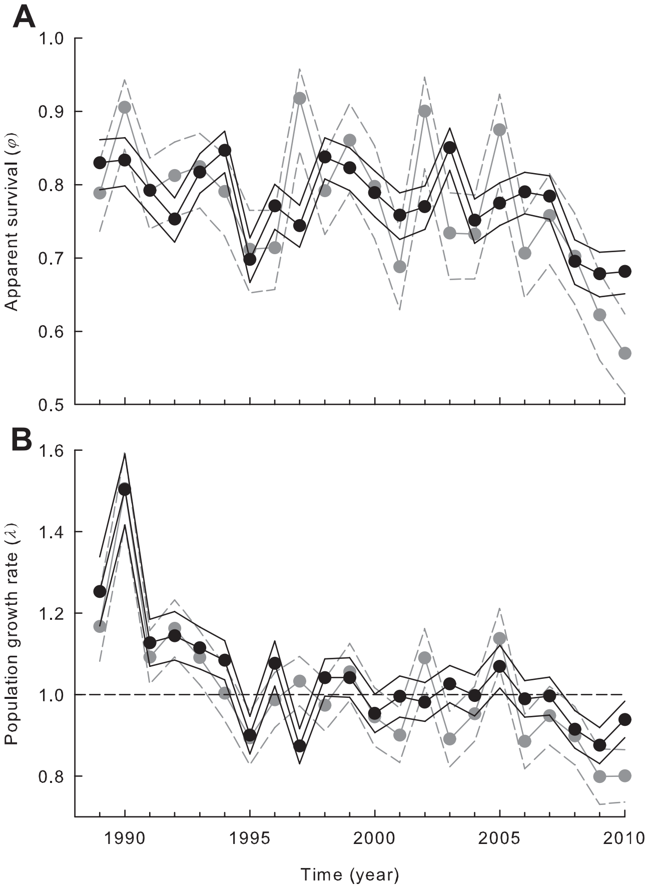

Figure 5. Residency patterns of breeding little penguins in natural burrows (grey symbols) and nest boxes (black symbols) between 1988 and 2010 on Phillip Island, Australia, estimated by the most supported Lin–Barker mark-recapture model described by (A) their apparent survival (φ; ±85% CI) and (B) rate of annual population growth (λ; ±85% CI).

greater reproductive output at artificial nest sites in some years and strong natal philopatry in little penguins (Dann 1992). Separation between breeding sites and foraging sites for seabirds may result in a density-independent relationship between penguin breeding density and breeding success. Because penguins forage at sea rather than where they breed, breeding area quality is not a reflection of potential foraging success, so potential breeding success and energetic costs should be the primary influence on their choice of breeding site. Species whose breeding-site quality is independent of foraging habitat quality may be more likely to benefit from nest-site provisioning.

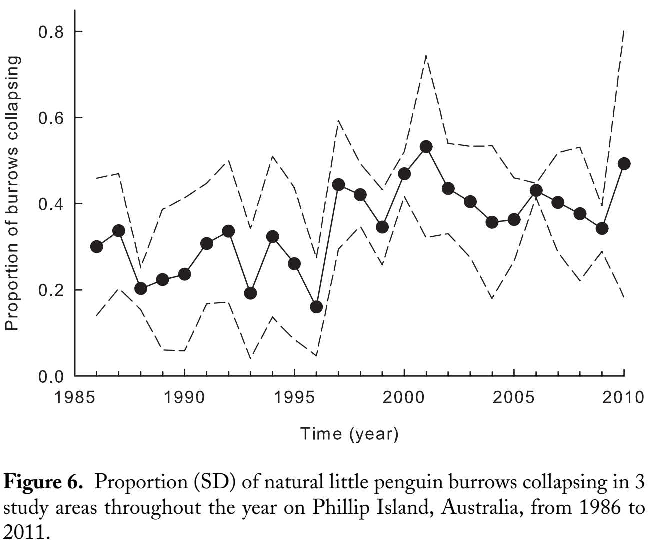

Figure 6. Proportion (SD) of natural little penguin burrows collapsing in 3 study areas throughout the year on Phillip Island, Australia, from 1986 to 2011.

Reproductive success of penguins was similar in nest boxes and natural burrows in most years, but in relatively poor breeding years, artificial nest boxes conferred an advantage for egg and chick survival. Hatching and fledging success was greater in nest boxes according to nest survival models and comparisons of productivity indices, though hatching success was similar between nest types when considering productivity indices. This disparity either suggests that penguins in natural burrows were more likely to hatch 2 eggs than in nest boxes when they were successful (nest survival models could not distinguish partial failures), or that a significant number of nest failures at natural nests were missed during monitoring and only by modeling nest survival rates were failures detected. Regardless, the combination of attractiveness and improved breeding performance imply penguins correctly assess nest boxes as conferring enhanced breeding success. Relative breeding success may be somewhat predictable from year to year between natural and artificial nest sites and penguins may be able to assess the breeding performance of conspecifics breeding in nest boxes and choose to breed there accordingly (i.e., the performance-based conspecific attraction hypothesis; Danchin et al. 1998).

We did not identify the proximal cause of clutch failures in natural and artificial nest sites during the study, but the difference in reproductive success suggests 1 or more of reduced nest predation, increased foraging success, improved microclimate conditions, or reduced nest abandonment was occurring at nest boxes in some years (Newton 1994*b*). Predation rates may be lower at nest boxes as has been observed for other bird species elsewhere (Fargallo 2001, Griffith et al. 2008, Catry et al. 2009, Llambias and Fernandez 2009), but we are unable to attribute failures to predation definitively with our monitoring. Intensive predator control, primarily for foxes, was undertaken on Phillip Island during the course of this study (Berry and Kirkwood 2010). Nest abandonment at natural nest sites was not driven by reduced foraging success given penguins from both nest types forage at sea away from their breeding areas. Nest boxes may improve microhabitat conditions for chicks by reducing flooding of nests which can affect natural nest sites, but nest boxes have been recorded exacerbating temperature fluctuations, which are detrimental for penguin chicks (Ropert-Coudert et al. 2004, Lei et al. 2014).

Reproductive output may be reduced at natural burrows because of nest abandonment at natural nest sites. An average of 35% of natural burrows collapsed each year, either during the breeding or non-breeding seasons, and this could have resulted in reduced hatching or fledging success, as found for African penguins (Seddon and Heezik 1991). If this was the main driver of clutch failure, years where differences in breeding success between natural burrows and artificial nest boxes (Fig. 3) would correspond with years of high burrow collapse rates (Fig. 6) which appeared to be true only in 1999, 2001, 2002, and 2010. Our study showed lower re-sighting rates of penguins at natural burrows, potentially as a result of natural burrows collapsing and penguins moving to alternative burrows to attempt breeding. Some of these alternative burrows were not monitored. However, apparent survival rates were similar at natural burrows and artificial nest boxes (Fig. 5A), indicating that many individuals that moved to unmonitored burrows returned to monitored burrows in later years. That re-sighting rates were greater for males than females is consistent with the observation that males establish nest sites and seek to attract females to their nest, thus exhibiting greater nest-site fidelity (Reilly and Cullen 1981). Hence, the probable reasons that breeding performance was enhanced at nest boxes in some years were reduced rates of egg or chick depredation and reduced rates of nests collapsing. This culminated in greater mean annual population growth rate in areas with artificial nests than natural burrows. The decline in growth rates between 2007 and 2010 (Fig. 5B) is driven by lower apparent survival at study areas in these years. This trend is mirrored in population estimates through 27 years of an increasing trend, a leveling off, and a recent decrease for this population (Sutherland and Dann 2014).

To improve conservation outcomes for cavity-nesting species using nest boxes, we see a need to predict the conditions that will lead to ecological traps (Battin 2004). Fletcher et al. (2012) suggested that ecological traps are more likely after degradation of existing habitats than after establishment of novel environments such as nest boxes; however, ecological traps are still possible after the introduction of novel habitats (Pöysä and Pöysä 2002, Mänd et al. 2005, Klein et al. 2007, Rodriguez et al. 2011). Ecological traps as a result of providing artificial nest sites may be more likely for populations that use the same habitats for breeding and foraging, as is the case for many terrestrial populations (e.g., Pöysä and Pöysä 2002, Mänd et al. 2005), because adopting a habitat with an artificial nest site will directly influence foraging success and hence breeding success. Foraging and breeding habitats are independent for seabirds, so providing artificial nest sites should not influence foraging success. Assessing breeding productivity and adult residency patterns for populations whose breeding and foraging habitats are either dependent or independent and whose breeding habitat is either degraded or novel will help to identify commonalities that lead to ecological traps associated with some nest box programs.

MANAGEMENT IMPLICATIONS

The provision of artificial nest boxes is an effective conservation strategy for little penguins in the short to long term where a shortage of suitable breeding habitat limits local recruitment and abundance. Nest-box provisioning for little penguins overcomes local nest-site limitation, improves breeding success in poor years, results in local population increase and hence, is not indicative of an ecological trap. However, the provision of nest boxes should not be considered a permanent solution. A self-sustaining local population in the long term will require that the causes of breeding site shortage are addressed so that populations that have become reliant on the provisioning of nest sites can transition from artificial back to natural nest sites. Encouragingly, the continued use of natural nests in the presence of artificial nests and the similar apparent survival at natural sites suggests little penguins could be weaned from artificial nests. Habitat restoration and mitigation of threats (land-based predators, marine pollution, and competition for prey) are likely to be the most effective means of conserving this population in the long term (Dann 1992, Mänd et al. 2005).

ACKNOWLEDGMENTS

We thank L. Renwick, P. Wasiak, and M. Healy for invaluable assistance in the field and valuable comments from M. Weston, B. Hansen, R. Sherley, and an anonymous reviewer on an earlier draft.

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Associate Editor: Courtney Amundson.