

The influence of surrounding habitat, behaviour and interspecific competition on nestbox use by endangered Glossy Black Cockatoos (*Calyptorhynchus lathami halmaturinus*)

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Nestboxes have been deployed for parrots and cockatoos (Psittaciformes) worldwide, but there is limited evidence of their efficacy for these species. We examined the use of nestboxes by endangered South Australian Glossy Black Cockatoos *Calyptorhynchus lathami halmaturinus*, a habitat specialist that feeds almost solely on the seeds of Drooping Sheoak *Allocasuarina verticillata* trees, and investigated the factors that influenced nestbox use. Between 1998 and 2017, the mean annual proportion of nesting attempts that successfully fledged a chick was similar in nestboxes (52%, $n = 547$) and natural hollows (53%, $n = 627$). Nestbox use increased over time, which may reflect changes in the size and extent of the Glossy Black Cockatoo population over the study period. Nestboxes were more likely to be used by Glossy Black Cockatoos if they were close to the nest of another breeding pair and were not occupied by Yellow-tailed Black Cockatoos *Zanda funerea* early in the breeding season. Nestboxes were also more likely to be used if they had been used in the previous breeding season, indicating nest-site fidelity. The amount of *A. verticillata* feeding habitat in a 1-km and 5-km radius did not significantly influence nestbox use. Our study provides further evidence of the value of nestboxes to cockatoo conservation programmes, but also suggests that multiple factors other than local food availability influence uptake by a target species. Given that Glossy Black Cockatoos prefer to aggregate their nests, nestboxes for this species are most likely to be beneficial when they are used to expand the capacity of existing breeding areas or are clustered in the landscape. Our study demonstrates that well-designed nestbox deployments should consider the preferred social groupings of cockatoos during the breeding season, and the location of competitor species, in order to maximize nestbox uptake.

Keywords: artificial hollow, Cacatuidae, competition, nestbox, Psittaciformes.

Tree hollows (also termed tree cavities) are used for nesting by around 18% of bird species globally and provide critical shelter and habitat for various species of mammals and invertebrates (Ranius 2002, Goldingay 2009, 2011, van der Hoek *et al.* 2017). However, natural tree hollows and the large, old trees in which they occur are a declining resource (Lindenmayer & Wood 2010, Lindenmayer *et al.* 2012). Tree hollow availability in landscapes can decline in response to human disturbance

(Gibbons *et al.* 2010, Saunders *et al.* 2014, McLean *et al.* 2015), fire interval and severity (Lindenmayer *et al.* 2016, Salmona *et al.* 2018), and also competition with other hollow-dependent species (Pell & Tidemann 1997, Dodaro & Battisti 2014). The global decline in hollow-bearing trees means that nest-sites could become limiting for species that are dependent on hollows (Newton 1994, Fischer *et al.* 2010). As a result of the long time frames associated with the restoration of hollow-bearing trees (Wormington & Lamb 1999, Ranius *et al.* 2009), nestboxes are commonly deployed as a short-term substitute for natural hollows.

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All 21 extant cockatoo species (Cacatuidae) and 93% of parrot species (Psittacidae) use tree hollows for nesting (van der Hoek *et al.* 2017). A number of conservation programmes have deployed nestboxes for parrots and cockatoos (Vaughan *et al.* 2003, Downs 2005, White *et al.* 2005), but uptake by target species can sometimes be low (Brightsmith & Bravo 2006). It has yet to be established whether nestboxes are an effective substitute for natural hollows for these species (Sutherland *et al.* 2020). Only a few studies to date have investigated whether breeding success in nestboxes is comparable to that in natural hollows, or the factors that influence nestbox usage (Sanz *et al.* 2003, Olah *et al.* 2014, Saunders *et al.* 2020). Nestboxes can also have problems; for example, they can be used by common or exotic species rather than the target species they were installed for, and usually require ongoing maintenance (Lindenmayer *et al.* 2017, Goldingay *et al.* 2018, Stojanovic *et al.* 2021). As nestboxes can be costly to instal and maintain, it is important to understand which factors increase the likelihood of use by the target species, and reduce the risk of occupancy by competitors (Goldingay & Stevens 2009, Lindenmayer *et al.* 2009).

The South Australian Glossy Black Cockatoo *Calyptrorhynchus lathami halmaturinus* (hereafter Glossy Black Cockatoo) is extinct on mainland Australia, and exists solely on Kangaroo Island, off the southern Australian coast (Mooney & Pedler 2005, Berris *et al.* 2018). Glossy Black Cockatoos nest in large tree hollows in the trunks or upper limbs of *Eucalyptus* trees, which are created when a fallen branch exposes the heartwood of a tree, and fungi or termite activity then lead to the creation of a hollow at that point (Garnett *et al.* 1999). Nestboxes have been installed for this species as part of a long-term recovery programme to alleviate a possible natural tree hollow shortage (Berris *et al.* 2018). Glossy Black Cockatoos feed almost exclusively on the seeds of Drooping Sheoak *Allocasuarina verticillata* trees, so proximity to *A. verticillata* woodlands is probably important in nest-site selection (Pepper 1997, Pepper *et al.* 2000, Chapman & Paton 2005, 2006). Indeed, clearance of this tree probably caused the extinction of the mainland South Australian Glossy Black Cockatoo population (Berris *et al.* 2018). However, some unused nestboxes are close to significant patches of *A. verticillata* (Crowley *et al.* 1998), so other factors must also drive

nest-site selection. A previous study of the breeding biology of Glossy Black Cockatoos found that natural nests were clustered (Garnett *et al.* 1999), but it is not known whether this was due to behaviour, or a clustering of hollow-bearing trees in the landscape. Several other species of hollow-nesting birds on Kangaroo Island may compete with Glossy Black Cockatoos for hollows (Garnett *et al.* 1999, Mooney & Pedler 2005). Approximately 39% of Glossy Black Cockatoo nests were destroyed during the 2019/20 Australian Black Summer bushfires (Berris *et al.* 2020), and nestbox installations are part of the post-fire recovery effort. It is therefore important to determine which factors influence nestbox use in this species so that nestboxes can be placed where they are of most benefit.

The aim of this study was to compare breeding success and nest occupancy rates between nestboxes deployed for Glossy Black Cockatoos and natural tree hollows, and to determine which factors influence nestbox occupancy rates. We also investigated whether nestbox use varied between two time periods during which population counts of Glossy Black Cockatoos differed. Given that Glossy Black Cockatoos are dietary specialists and natural nests tend to be clustered in the landscape, we hypothesized that the amount of *A. verticillata* feeding habitat in the surrounding area and proximity to other nesting pairs would influence nestbox occupancy by Glossy Black Cockatoos. We also examined whether the presence of nest competitors, female natal nest type (tree hollow versus nestbox) and previous nestbox use influenced occupancy of nestboxes.

METHODS

Study species

The remaining population of Glossy Black Cockatoos tends to congregate along the north coast and some inland rivers of Kangaroo Island, close to where *A. verticillata* woodlands are located (Mooney & Pedler 2005; Fig. 1). As a result of a long-term recovery programme, the population has increased from fewer than 200 individuals in 1996 to more than 350 birds in 2016 (Berris *et al.* 2018).

Glossy Black Cockatoos lay a single egg between January and July, and most pairs nest once per year (Garnett *et al.* 1999). Common

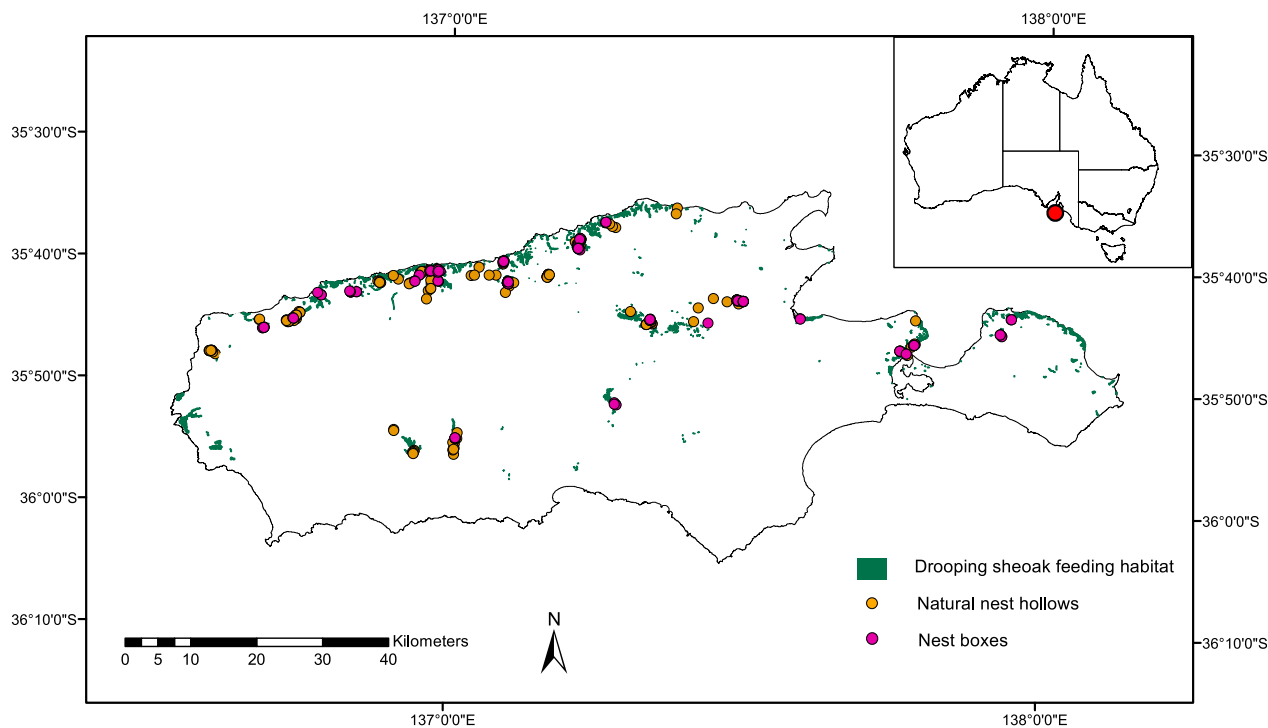


Figure 1. Kangaroo Island, located approximately 13 km off the coast of southern Australia, showing the location of Glossy Black Cockatoo natural nests, nestboxes and *Allocasuarina verticillata* feeding habitat.

Brushtail Possums *Trichosurus vulpecula* are known to cause significant predation losses of eggs and nestlings, so all known nest trees are protected from possum access (Garnett *et al.* 1999, Berris *et al.* 2018). Glossy Black Cockatoos have previously been observed to nest in a clustered fashion in the landscape, although aggression has also been noted between breeding females (Garnett *et al.* 1999). There is evidence that Yellow-tailed Black Cockatoos, Galahs *Eolophus roseicapilla* and feral Honey Bees *Apis mellifera* compete for tree hollows with Glossy Black Cockatoos, although the above birds and most other hollow-nesting bird species on Kangaroo Island tend to nest between July and February (Garnett *et al.* 1999, Berris & Barth 2020). Consequently, interspecific competition for tree hollows experienced by Glossy Black Cockatoos is probable only for short periods during the early or late parts of their nesting season.

Study area

The study took place on Kangaroo Island (4405 km²), located approximately 13 km off the

coast of South Australia (Fig. 1). The island experiences a Mediterranean climate, with rainfall predominantly during the winter months (June–August) (Colls & Whitaker 2012). Natural tree hollows and nestboxes installed by the recovery programme are mostly located in tall, closed woodlands dominated by *Eucalyptus cladocalyx*, and in creek lines containing *Eucalyptus leucoxylon* and *Eucalyptus camaldulensis*. Tree hollows used by Glossy Black Cockatoos and nestboxes installed for the species are generally close to *A. verticillata* woodlands (Fig. 1).

Nestbox details

Nestboxes installed on Kangaroo Island are constructed of polyvinyl chloride (PVC) stormwater pipe (300-mm internal diameter) cut to 1-m lengths (Pedler 1996). A 16-cm-wide and 20-cm-long entrance is cut out of the top end of the pipe (Fig. 2). Nestboxes initially had metal mesh floors and a single piece of 3.2-mm fencing wire as an internal climbing ladder (Pedler 1996). However, from 2015 onwards, PVC endcaps replaced mesh floors which were rusting and collapsing over time,

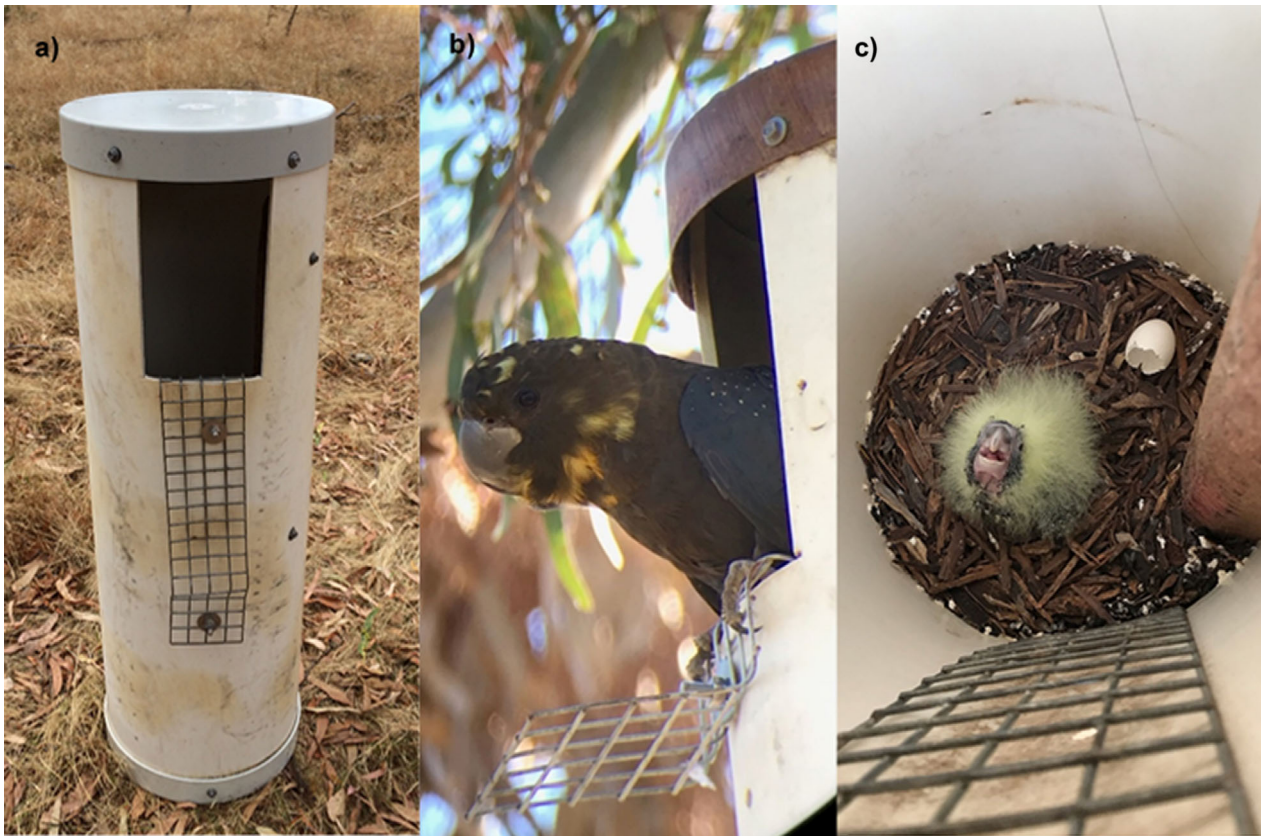


Figure 2. Examples of nestboxes installed for Glossy Black Cockatoos. (a) A PVC nestbox before being installed in a tree. (b) A female Glossy Black Cockatoo at the entrance to a nestbox. Females will generally come to the entrance of nestboxes when the base of the tree is tapped, and a female inside a nest during the day is probably a sign of egg incubation or brooding a small nestling. (c) A Glossy Black Cockatoo nestling inside a nestbox.

and internal single-wire climbing ladders were changed to galvanized steel mesh, which is more robust (Fig. 2). A weatherproof lid constructed of either metal or PVC is affixed to each nestbox. A small number of nestboxes used in this study ($n = 17$) were constructed from wooden logs or timber slats. These nestboxes also have similar entrance sizes, dimensions and lids as described for the PVC nestboxes. Nestboxes were installed in *E. cladocalyx*, *E. leucoxydon* or *E. camaldulensis* trees that were close to either natural tree hollows or feeding habitat used by Glossy Black Cockatoos. Nestboxes were installed on the trunks of live trees, usually 5–19 m from the ground. Although data could not be obtained on the precise installation date for all nestboxes installed during the 1990s, we had data for 56 nestboxes that were installed by 2000, and the number installed had increased to 129 by the end of 2017.

Nest monitoring protocol

Natural tree hollows and nestboxes were checked for occupancy approximately monthly during the nesting season (late January to July/August) by staff and volunteers of the recovery programme. Nests were assumed to be at incubation or small hatchling stage if a female was occupying the nest during the day. Occupancy was confirmed by tapping the base of the nest tree, which usually results in a female coming to the entrance of an occupied nest if incubating an egg (Fig. 2b), or by observing a female leaving the nest briefly in the evening to be fed by a male. When a female left its nest to be fed, the presence of an egg could be confirmed by either climbing the nest tree or using an infrared nest inspection camera on an 18-m extendable pole. Nestlings were confirmed by: (1) an observer hearing a nestling call from a nest or

observing a nestling near the entrance, (2) by climbing the nest tree or (3) by using an infrared nest inspection camera mounted on an 18-m extendable telescoping pole during the day when parent birds were away feeding. Nests were monitored until an outcome of success (large nestling seen at entrance, nestling fledged, nest checked and empty after expected fledging date with no evidence of mortality) or failure (unhatched egg, evidence of broken/smashed egg or dead nestling) was recorded. If other species were encountered using nestboxes, they were recorded. Nestlings of over 250 g in weight were banded where practicable (if the nest tree was safe to climb and climbing did not pose a disturbance risk to other nesting pairs) with a uniquely numbered stainless steel leg band (size 21) provided by the Australian Bird and Bat Banding Scheme.

Data analysis

All statistical analyses were performed using R (version 4.0.0, R Core Team 2020). All mean values are given in the form mean \pm standard error (se). Nest monitoring data were compiled for all available years (1998–2017) for monitored nestboxes and tree hollows. Data on the breeding success of occupied nests were available for all years. The influence of nest type (natural hollow or nestbox) was investigated using binomial generalized linear mixed models (GLMMs; family = binomial, link = logit) with nest outcome (1 = success, 0 = failure) as the response variable and nest type (natural hollow or nestbox) and year (1998–2017) as categorical fixed effects. Individual nestbox/natural nest ID was included as a random effect to account for pseudo-replication caused by repeat observations from the same nests in different years. Nests were each assigned to a region, which was also included as a random effect to account for spatial pseudo-replication. Seven geographical regions were used and were based on flock regions reported in Mooney and Pedler (2005), except that the large eastern flock region was divided in two to broadly represent different catchment areas on the island.

Nest occupancy data were compiled by categorizing each monitored nest as used or not in any one year. In some years, nests that were inactive early in the breeding season were monitored too infrequently later in the season to adequately determine whether they had not been used by

Glossy Black Cockatoos, and a failed late nesting attempt could have been missed. However, reliable absence data were available for 2000–04 and 2009–17. Glossy Black Cockatoos also had an increasing population trend between 2000 and 2017, which may have influenced nest occupancy. We therefore compared occupancy rates between nest types (nestboxes and natural hollows) and between two time periods (2000–04 and 2013–17). Data from 2000 to 2004 represented a period when nestboxes were relatively new in the landscape, and the population was still in its early stages of recovery (≤ 280 individuals recorded each year, Berris *et al.* 2018). Data from 2013 to 2017 reflected a period when nestboxes had been present in the landscape for over 10 years, and more than 300 individuals were recorded each year (Berris *et al.* 2018). Binomial GLMMs (family = binomial, link = logit) were used to investigate the influence of nest type (natural hollow or nestbox) and time period (early = 2000–04 and late = 2013–17) on nest occupancy by Glossy Black Cockatoos, with individual nestbox/natural nest ID and region both included as random effects.

Data from 2013 to 2017 were then used to investigate factors that influence nestbox use, as the population size during this period most resembled the current population size. The amount (in km²) of *A. verticillata* woodland (potential feeding habitat) and large *Eucalyptus* woodland (potential nesting habitat) in 1, 5 and 10-km radii around nestboxes was calculated for all nestboxes available between 2013 and 2017, using native vegetation spatial layers mapped by the Department for Environment and Water and ArcGIS (version 10.6.1). The amount of *A. verticillata* woodland in 5 and 10-km radii were strongly positively correlated, so only the amount in a 1-km and a 5-km radius was used for the final analysis. The amount of large *Eucalyptus* woodland in 1, 5 and 10-km radii was also strongly positively correlated so only the amount in a 1-km radius was used. The number of other active Glossy Black Cockatoo nests within a 1-km radius and the distance to the nearest other known active nest was also calculated for all nestboxes for each year. Binomial GLMMs (family = binomial, link = logit) were used for analysis, with nest occupancy (1 = occupied in a given year, 0 = not occupied) used as the response variable. We included *A.verticillata_1km*, *A.verticillata_5km*, *Euc_1km*, *Nests_1km* and *Nest_distance* as

Table 1. Fixed effects included in the global model (generalized linear mixed models; family = binomial, link = logit) of nestbox use by Glossy Black Cockatoos.

Effect name	Definition and data type
<i>A.verticillata_1km</i>	The amount (in km ²) of <i>Allocasuarina verticillata</i> woodland (potential feeding habitat) in a 1-km radius in km ² (continuous)
<i>A.verticillata_5km</i>	The amount (in km ²) of <i>A. verticillata</i> woodland (potential feeding habitat) in a 5-km radius in km ² (continuous)
<i>Euc_1km</i>	The amount (in km ²) of large <i>Eucalyptus</i> woodland (potential nesting habitat) in a 1-km radius in km ² (continuous)
<i>Nests_1km</i>	The number of other active Glossy Black Cockatoo nests in a 1-km radius (continuous)
<i>Nest_distance</i>	Distance to the nearest other active Glossy Black Cockatoo nest in km (continuous)
<i>YTBC</i>	Used by a Yellow-tailed Black Cockatoo (potential nest competitor) during the early breeding season (occupancy January onwards, (1) or not used that year (0) (binomial)
<i>Used_previous_year</i>	Used by a Glossy Black Cockatoo pair in the previous breeding season (1) or not used (0) (binomial)

continuous fixed effects, and *YTBC* and *Used_previous_year* as binomial fixed effects (see variable definitions in Table 1). Individual nestbox ID and region were again included as random effects.

All three binomial GLMM analyses followed the approach outlined by Grueber *et al.* (2011). First, global models were built using the *glmer* function in the R-package *lme4* (Bates *et al.* 2015), which included all fixed and random effects. Numeric and binary fixed effects were standardized as recommended by Gelman (2008), using the R-package *arm* version 1.12-2 (Gelman & Su 2021). The R-package *MuMIn* version 1.43.17 (Barton 2020) was then used to generate model sets that represented all possible combinations of fixed effects included in the global models, and to rank models. Models were ranked using the Akaike Information Criterion (Akaike 1973) with a correction for small sample sizes (AICC; Hurvich & Tsai 1989) and Akaike weights (ω). If no one model had more than 95% support based on the values of ω , then model sets containing models with an Δ AICC less than 2 were used to calculate model-averaged estimates for the fixed effects in the model sets. The sum of model weights of all models including each fixed effect was then used to calculate the relative importance of each fixed effect included in models in the model sets. We also calculated the coefficient of determination for each model in model sets, as well as the global models and the null models based on the methods outlined by Nakagawa *et al.* (2017) using the *MuMIn* package, which calculated the amount of variance explained by the fixed effects in each model.

A long-term dataset on banding records and band re-sightings was used to determine the nests

from which female nestlings fledged (natural hollow or nestbox) and what type of nest they subsequently used as adults. A Pearson χ^2 test with Yates continuity correction was used to test for an association between natal nest type and adult nest choice in female Glossy Black Cockatoos.

RESULTS

Nesting success in nestboxes and natural hollows

Between 1998 and 2017, 52% of nesting attempts in nestboxes resulted in a successful fledging ($n = 547$) and 53% of nesting attempts in natural tree hollows resulted in a successful fledging ($n = 627$). GLMM analyses of nesting success included only one model with a Δ AICC less than 2, and this model included only an influence of year on nesting success (see Supplementary material, Table S1). Nest type did not significantly influence nesting success, and both models that included nest type had a Δ AICC greater than 2. However, the proportion of variance explained by all models in the model set was low (0.09–0.15) and the model that contained nest type alone did not explain any more of the variance in the dataset than the null model (see Supplementary material, Table S1).

Occupancy of nestboxes and natural hollows

Occupancy of nestboxes was 0.21 ($n = 278$) between 2000 and 2004, and this increased to 0.44 ($n = 418$) between 2013 and 2017, whereas the occupancy of natural hollows was 0.29 ($n = 223$) between 2000 and 2004 and 0.27

Table 2. Avian species encountered in nestboxes during the Glossy Black Cockatoo nesting season (late January to August) between 2013 and 2017, and the number of times nesting attempts were recorded. For nocturnal Eastern Barn Owls and Australian Boobooks, which also use nestboxes for shelter during the day, the count is the number of nestboxes occupied or used for breeding by these species over the study.

Species	Number of nesting attempts/sheltering in nestboxes between 2013 and 2018
Glossy Black Cockatoo <i>Calyptorhynchus lathami halmaturinus</i>	183
Yellow-tailed Black Cockatoo <i>Zanda funerea</i>	81
Australian Shelduck <i>Tadorna tadornoides</i>	7
Eastern Barn Owl <i>Tyto javanica</i>	6
Galah <i>Eolophus roseicapilla</i>	4
Australian Boobook <i>Ninox boobook halmaturina</i>	2

($n = 480$) between 2013 and 2017. GLMM analyses of nest occupancy included only one model with a ΔAICC less than 2, and this model included a significant influence of time period (2000–04 or 2013–17) and an interaction between time period and nest type on nest occupancy (see Supplementary material, Table S2). Nest type was also included in the top candidate model, but it did not significantly influence nest occupancy on its own. Models that did not include the interaction between time period and nest type had a ΔAICC greater than 19. Nests were 3.5 times more likely to be occupied in the later time period (2013–17; estimate = -1.27 , se = ± 0.22 , $P < 0.001$), but in the later period natural nests were far less likely to be occupied than nestboxes, compared with the earlier period (estimate = -1.71 , se = ± 0.37 , $P < 0.001$).

Other species recorded using nestboxes

Glossy Black Cockatoos were recorded using 85 regularly monitored nestboxes 183 times between 2013 and 2017. Other bird species encountered using these nestboxes during the Glossy Black Cockatoo nesting season were: Yellow-tailed Black Cockatoos between January and May; Australian Shelducks *Tadorna tadornoides* and Galahs between July and September; and Eastern Barn Owl *Tyto javanica* and Australian Boobook *Ninox boobook halmaturina* between February and June (Table 2). Common Brushtail Possums were recorded using nestboxes on seven occasions when nest protection devices (tin tree collars and pruned canopies) had failed. On at least three occasions, Glossy Black Cockatoos successfully fledged a young after a Yellow-tailed Black Cockatoo young was confirmed to have fledged from a nestbox,

indicating that it was possible for a successful nesting attempt to occur for both species in the one nestbox in a 12-month period.

Factors that influenced nestbox use in Glossy Black Cockatoos

GLMM analyses of nestbox use included six top candidate models that had a ΔAICC less than 2. The top six candidate models had ω values of between 0.18 and 0.07 and all included an influence of *Used_previous_year*, *YTBC* and *Nest_distance* (Table 3). Models that did not include all three of those parameters all had a ΔAICC of 3.7 or more, and models that did not include both *Used_previous_year* and *YTBC* all had a ΔAICC greater than 18. The proportion of variance explained by the fixed effects in the six top candidate models was between 0.31 and 0.32 (Table 3). The proportion of the variance explained by the six top candidate models improved to 0.56–0.59 for all models when the random effects of nestbox ID and region were included in the calculation.

The most important predictors of nestbox use by Glossy Black Cockatoos were *Used_previous_year*, *YTBC* and *Nest_distance* (Table 4), which were similarly important. Other parameters included in the top six candidate models (*A.verticillata_5km*, *A.verticillata_1km*, *Euc_1km*, *Nests_1km*) did not significantly influence nestbox use (Table 4). Nestboxes were almost six times more likely to be used by Glossy Black Cockatoos in a given year if they had been used in the previous breeding season and were 86% less likely to be used by Glossy Black Cockatoos if occupied by Yellow-tailed Black Cockatoos early in that same breeding season (Fig. 3). Each 1-km

Table 3. Top candidate model set for factors that influence the use of nestboxes by Glossy Black Cockatoos, including the global model and intercept-only model. The marginal R^2 is provided, which gives the proportion of variance explained by the fixed effects in the models. Definitions of parameter names are provided in Table 1.

Model parameters	df	AIC _C	ΔAIC _C	ω	R ²
<i>Used_previous_year</i> + <i>YTBC</i> + <i>Nest_distance</i> + <i>A.verticillata_5km</i>	7	404.2	0.00	0.18	0.31
<i>Used_previous_year</i> + <i>YTBC</i> + <i>Nest_distance</i> + <i>Euc_1km</i> + <i>A.verticillata_1km</i> + <i>A.verticillata_5km</i>	9	405.4	1.19	0.10	0.32
<i>Used_previous_year</i> + <i>YTBC</i> + <i>Nest_distance</i>	6	405.6	1.38	0.09	0.31
<i>Used_previous_year</i> + <i>YTBC</i> + <i>Nest_distance</i> + <i>A.verticillata_1km</i> + <i>A.verticillata_5km</i>	8	405.9	1.62	0.08	0.31
<i>Used_previous_year</i> + <i>YTBC</i> + <i>Nest_distance</i> + <i>Nests_1km</i> + <i>A.verticillata_5km</i>	8	405.9	1.64	0.08	0.31
<i>Used_previous_year</i> + <i>YTBC</i> + <i>Nest_distance</i> + <i>Euc_1km</i> + <i>A.verticillata_5km</i>	8	406.2	1.91	0.07	0.32
<i>Used_previous_year</i> + <i>YTBC</i> + <i>Nest_distance</i> + <i>Euc_1km</i> + <i>A.verticillata_1km</i> + <i>A.verticillata_5km</i> + <i>Nests_1km</i> (global model)	10	407.1	2.84	0.04	0.32
Intercept (null model)	3	446.5	42.25	0.00	0.00

Table 4. Model-averaged estimates of the effect of different factors on nestbox use by Glossy Black Cockatoos using the seven top candidate models, including the relative importance of different factors. The adjusted standard error (se) is reported, and estimates were calculated using a full (not conditional) average. Definitions of parameter names are provided in Table 1.

Parameter	Estimate	se	z-value	Pr(> z)	Relative importance
(Intercept)	−0.274	0.442	0.621	0.535	
<i>Used_previous_year</i>	1.783	0.360	4.952	<0.001	1.00
<i>YTBC</i>	−1.934	0.424	4.557	<0.001	1.00
<i>Nest_distance</i>	−1.239	0.575	2.154	0.031	1.00
<i>A.verticillata_5km</i>	1.109	0.866	1.281	0.200	0.85
<i>A.verticillata_1km</i>	−0.288	0.672	0.428	0.669	0.30
<i>Euc_1km</i>	0.247	0.631	0.391	0.696	0.28
<i>Nests_1km</i>	−0.046	0.226	0.204	0.838	0.13

increase in the distance from another active Glossy Black Cockatoo nest was associated with a 71% decrease in the likelihood of use of a nestbox (Fig. 3).

Effect of natal nest on nest choice

Since 1996, 43 females were leg-banded as nestlings and subsequently identified nesting as adults

Table 5. The nest choice of banded adult female Glossy Black Cockatoos that fledged from 1996 onwards by natal nest type (nestbox or natural hollow).

Natal nest	Nest type used for breeding as an adult	
	Nestbox	Natural hollow
Nestbox	28	27
Natural hollow	50	66

on 171 occasions. There was no association between natal nest type and nest choice in adult females (Pearson $\chi^2 = 0.63$, $P = 0.43$; Table 5).

DISCUSSION

Our results demonstrate that nestboxes are an effective solution to the problem of natural hollow shortages for Glossy Black Cockatoos, with no apparent adverse impacts on nesting success. Similar findings have also been reported in Carnaby's Black Cockatoos *Zanda latirostris* and Scarlet Macaws *Ara macao* (Olah *et al.* 2014, Saunders *et al.* 2020). Nestbox use by Glossy Black Cockatoos was influenced by multiple factors in our study, primarily use by conspecifics in the previous breeding season and proximity to other breeding pairs (both positive effects), and competition with Yellow-tailed Black Cockatoos (a negative effect).

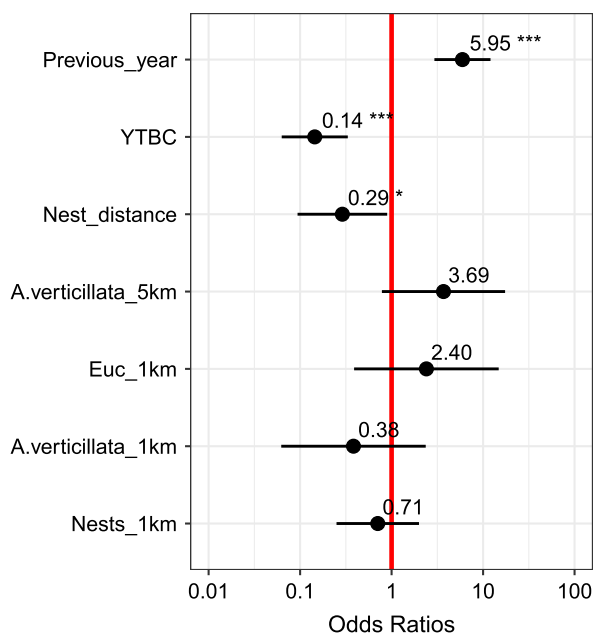


Figure 3. Forest plot of the odds ratio (and 95% confidence interval) of fixed effects included in the seven top candidate models of nestbox use by Glossy Black Cockatoos based on model averaging. The red vertical intercept (odds ratio = 1) indicates no effect. Asterisks indicate the significance level of *P* values (**P* < 0.05; ****P* < 0.001).

Our results indicated that natal nest type did not influence nest choice in Glossy Black Cockatoos. Given that Glossy Black Cockatoos prefer to aggregate their nests in the landscape, future nestbox installations for this species will probably be of most benefit when they are used to expand the capacity of existing breeding areas or are clustered in the landscape.

Nestboxes were more likely to be used if they were closer to the active nest of another Glossy Black Cockatoo pair. However, the amount of *A. verticillata* feeding habitat in a 1 and 5-km radius did not significantly influence nestbox use despite this tree being the main food source. This indicates that factors other than food availability were driving nest clustering in the landscape. Red-tailed Black Cockatoos *Calyptrorhynchus banksii naso*, the closest living relative of Glossy Black Cockatoos, have also been observed to cluster their nests in the landscape (White *et al.* 2011, Johnstone *et al.* 2013). Cockatoos are highly social, with some species exhibiting long-term pair bonds as well as stable social bonds with individuals beyond pair bonds (Saunders 1982, Garnett *et al.* 1999, Aplin *et al.* 2021). It could be that

social bonds between individuals, outside pair bonds, drive this behaviour. Another possible explanation could be that individuals prefer to nest close to their natal nesting area, causing a clustering of nesting activity in the landscape over time. Clustering nesting may allow pairs to travel between feeding and nesting grounds in flocks, which thereby reduces the risk of predation by raptors. Female aggression at nest trees has been observed (Garnett *et al.* 1999, K. Berris, pers. obs.) so it is possible that although pairs nest in close proximity to one another, there is competition between them for preferred nests. Research on the social interactions and social bonds between non-pair flock members in Glossy Black Cockatoos is required to provide further insights into what is driving nest clustering in this species.

Our hypothesis that the amount of feeding habitat in the surrounding area was one of the major drivers of nestbox use was not supported. Although Glossy Black Cockatoos feed almost exclusively on *A. verticillata* seeds, in our study some nestboxes had no *A. verticillata* feeding habitat within either a 1 or 5-km radius (Supplementary Material, Appendix S1) indicating that some pairs are flying more than 5 km daily to access food. Glossy Black Cockatoos have been recorded regularly flying up to 12 km from nests to feed (Crowley *et al.* 1998), supporting our finding that the amount of feeding habitat in close proximity to nests is not all that is driving nestbox use.

Nestboxes that were used in the previous year were more likely to be used the following year, indicating nest-site fidelity. The *A. verticillata* trees flower and produce seed annually, and cones that hold seed are retained on the tree until they dry out because of stem death, fire or are removed from the tree (Moncur *et al.* 1997, Pepper 1997). It is likely that nest-site fidelity reflects the stability of this food source, even if it is some distance away. Significant areas of *A. verticillata* feeding habitat were burnt during the 2019/20 bushfires, and will be unavailable as a food source for at least 10 years until woodlands regenerate (Mooney & Pedler 2005). Some nesting areas were deserted following previous fires in 1991 that significantly reduced feeding habitat in the far western part of Kangaroo Island (Crowley *et al.* 1998). Therefore, although our analysis indicated that the amount of *A. verticillata* feeding habitat in 1 and 5-km radii did not significantly influence nestbox use, it is probable that proximity to substantial feeding

habitat might. As nestboxes in this study were all installed within 10 km of feeding habitat, we could not determine the maximum distance that Glossy Black Cockatoos will travel to forage. It is important that post-fire nestbox installations are planned in locations where Glossy Black Cockatoos continue to nest post-fire as some areas that are too far away from feeding habitat may be vacated following bushfires.

The occupancy of nestboxes increased over time in the Glossy Black Cockatoo population. One possible explanation for the observed difference in nestbox use over time could be increasing intraspecific competition for hollows in some areas as the population increased, which is consistent with birds aggregating to nest. Given that natal nest type did not influence nest choice in adult females, and some nestboxes were used shortly after installation between 2000 and 2004, it is unlikely that the PVC design of nestboxes was off-putting to Glossy Black Cockatoos. We therefore postulate that the observed differences in nestbox use over time were driven at least in part by natural hollows becoming limiting as the Glossy Black Cockatoo population increased. Increasing nestbox use over time has also been observed in an increasing population of the critically endangered Echo Parakeet *Psittacula eques* (Tatayah *et al.* 2007). It could be that tree hollow shortages are not evident initially in some species because the populations are small and/or declining. In successful parrot and cockatoo recovery projects, tree hollow shortages may only become apparent once the population size has increased.

Our analysis included a comparison of the amount of large *Eucalyptus* woodlands within the vicinity of nestboxes as a proxy for potential nesting habitat, but this did not influence nestbox use in our study. However, further research is required on the availability of natural hollows within these woodlands as habitat quality may vary widely depending on previous logging history or fire frequency and intensity. On Kangaroo Island, large *E. cladocalyx* trees were extensively cleared within woodlands for mine and sleeper timber during the island's early settlement (Bauer 1959). Clearance was selective, and large trees were targeted to such an extent that in the 1950s it was estimated that most *E. cladocalyx* that remained were smaller, younger trees (Bauer 1959). Given that the large hollows used by Australian parrots and cockatoos are mostly in trees that are at least 200 years old

(Mawson & Long 1994, Johnstone *et al.* 2013), Kangaroo Island may still have a hollow deficit because of previous logging activity. Our study did not investigate natural hollow availability in *Eucalyptus* woodlands on Kangaroo Island, but this could be an area of future research.

The main other species using nestboxes during the Glossy Black Cockatoo nesting season was Yellow-tailed Black Cockatoo. Yellow-tailed Black Cockatoo nestlings occupied nestboxes as late as May, and in these cases the nestbox was unavailable for a large part of the Glossy Black Cockatoo nesting season. Yellow-tailed Black Cockatoos were generally only recorded using nestboxes on the western half of Kangaroo Island, and were not recorded nesting in some areas further east. There has been a suggestion that breeding of Yellow-tailed Black Cockatoos on Kangaroo Island may have only begun in recent decades in response to the establishment of large commercial pine plantations, which provided an additional food source for this species (Crowley *et al.* 1998). A small trial in which nestboxes were closed during the Yellow-tailed Black Cockatoo nesting season indicated that opening nestboxes in January, after the period when most Yellow-tailed Black Cockatoos have laid eggs, could increase Glossy Black Cockatoo nestbox occupancy (Crowley *et al.* 1998). Other options could be to provide additional nestboxes in areas where Yellow-tailed Black Cockatoos are present. Large areas of commercial pine plantations on Kangaroo Island were burnt during the 2019/20 Black Summer Bushfires, so future work could investigate whether there is a reduction in breeding by Yellow-tailed Black Cockatoos in nestboxes post-fire. It could be that competition with this species for nestboxes is reduced post-fire.

Our study was unable to detect the impact of interference competition with Galahs and Little Corellas *Cacatua sanguinea* with our sampling methods and frequency. Few records of Galahs and no records of Little Corellas were recorded in nestboxes in our study, probably because these species tend to nest from September to December. However, Galahs frequent nests outside their breeding season and have been suspected of destroying Glossy Black Cockatoo eggs, and Little Corellas have been implicated in the death of late-season Glossy Black Cockatoo nestlings (Garnett *et al.* 1999). Both of these species have self-colonized Kangaroo Island and have increased

significantly since they were first detected (Baxter 2015). Their population trajectory and potential impact on the Glossy Black Cockatoo population warrants further research.

The variation in nestbox use explained by the six top candidate models improved when nestbox ID and region were included as random effects. This indicates that other properties of individual nestboxes or regions on Kangaroo Island that we did not measure could be influencing nestbox use. Most nestboxes were of a similar design (PVC), but they were installed at different heights and the entrances faced in different directions as a result of differences in the size and shape of the trees in which they were installed. A possible area of future research could therefore be to determine whether the height or aspect of nestboxes influences their use by Glossy Black Cockatoos.

Our study shows that nestboxes are now being regularly used by the Glossy Black Cockatoo population and that nesting success rates are similar between nestboxes and natural hollows. Other studies have found that the thermal properties of nestboxes can be inferior compared with natural hollows, which can influence nestling growth rates in other species (Larson *et al.* 2015, Griffiths *et al.* 2017, Rowland *et al.* 2017). Alteration of existing standing trees to create natural hollows could be an alternative to nestboxes, and generally result in better thermal properties, and such sites may be less conspicuous in natural landscapes (Brightsmith & Bravo 2006, Griffiths *et al.* 2018, 2020). However, the advantage of nestboxes is that they can be installed in landscapes where the trees are not large enough to support natural hollows. There was no evidence in our study that nesting attempts in nestboxes were any more likely to fail than nesting attempts in natural hollows. However, around half of all eggs laid failed to fledge, regardless of nest type, and models with nest type and year as fixed effects explained very little of the variance in the data, indicating that other factors that we did not measure were influencing nesting success. All of the nests were protected from Common Brushtail Possum predation, so this can be excluded as a possible cause of nest failure. Given the small population size of Glossy Black Cockatoos on Kangaroo Island, it is important to investigate the causes of nest failure in both nestboxes and natural hollows, to determine if further management actions could improve recruitment in this species.

CONCLUSIONS

Our study provides further evidence of the value of nestboxes to cockatoo conservation programmes. Our results suggest that multiple factors influence uptake by a target species. Nestboxes were more likely to be used by Glossy Black Cockatoos if they were close to other nesting pairs and were not used by competitor species. Given that Glossy Black Cockatoos prefer to aggregate their nests in the landscape, nestboxes for this species are most likely to be beneficial when they are used to expand the capacity of existing breeding areas or are clustered in the landscape. Our study demonstrates that well-designed nestbox deployments should consider the preferred social groupings of cockatoos during the breeding season, as well as food availability, to maximize nestbox uptake.

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ETHICAL NOTE

Data were collected under permits from the Wildlife Ethics Committee (Department of Environment and Water, South Australia) including permit numbers 1/2013 and 8/2016, and all research methods complied with the *Australian code for the care and use of animals for scientific purposes*, 8th edition (2013).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Karleah Berris: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Michael Barth:** Conceptualization (supporting); data curation (supporting); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (supporting); writing – review and editing (supporting). **Trish Mooney:** Conceptualization (supporting); data curation (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); writing – review and editing (supporting).

Data Availability Statement

The data that support the findings of this study are available in the supplementary material (Appendix S1 and Appendix S2) or from the corresponding author upon reasonable request (nesting success data and spatial data).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Model set generated to investigate the influence of nest type (nestbox or natural tree hollow) and year on nesting success in Glossy Black Cockatoos.

Table S2. Model set generated to investigate the influence of nest type (nestbox or natural tree hollow) and time period (2000–04 and 2013–17) on nest occupancy in Glossy Black Cockatoos.

Table S3. Estimates of the effect of nest type (natural tree hollow versus nestbox) and time period (2013–17 versus 2000–04) on nestbox use by Glossy Black Cockatoos using the top candidate model.

Appendix S1. Raw data of nestbox use by Glossy Black Cockatoos and the amount of *A. verticillata* in a 1- and 5-km radius, amount of large *Eucalyptus* habitat in a 1-km radius, number of other active Glossy Black Cockatoo nests in a 1-km radius, distance to nearest other Glossy Black Cockatoo nest, use in previous breeding season, use by Yellow-tailed Black Cockatoo that year and region. Area data are given in km² and distance data in km.

Appendix S2. Raw data of nest use by Glossy Black Cockatoos and nest type (natural hollow or nestbox), time period (2000–2004 or 2013–2017) and region.